

Founding of the
Maize Genetics Cooperation News Letter
at Cornell University
Volume II



Rollins Adams Emerson (1873–1947)

A 90th Anniversary Tribute

Edited by
Lee B. Kass
Edward H. Coe, Jr.
Michael N. Cook
Margaret E. Smith
Judy L. Singer

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*Rollins Adams Emerson (1873–1947), Head of Cornell University Department of Plant Breeding from 1914–1942
(Courtesy of Plant Breeding files, Cornell University)*

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Founding of the
Maize Genetics Cooperation News Letter
at Cornell University
A 90th Anniversary Tribute

Volume II



Thomas Hunt Morgan and Rollins Adams Emerson

Willard Straight Hall, Cornell University, Ithaca, New York.

Headquarters of the 1932 Sixth International Congress of Genetics, 24-31 August 1932.

Morgan was President of the Congress and Emerson the General Chairman of the Local Committee.

(Courtesy of Edward S. Buckler)

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Rollins Adams Emerson (1873-1947), Head of Cornell University Department of Plant Breeding from 1914–1942
(*Courtesy of Plant Breeding files, Cornell University*)

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1945 Synopsis Club group photo (*Reprinted from Murphy & Kass 2011, p. 157; Courtesy of Plant Breeding & Genetics and the publisher*)

Back Cover:
Maize Genetics Cooperation News Letter Volumes, compiled by R.A. Emerson (*Photo image by Judy Singer*)

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To the Legacy of R.A. Emerson



To Maize Cooperators Worldwide

Volume I

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FOREWORD

CELEBRATING 90 YEARS OF MAIZE COOPERATION

By

Dr. Edward S. Buckler

*Research Geneticist, U.S. Department of Agriculture - Agricultural Research Service,
Robert Holley Center, Cornell University; and
Adjunct Professor of Plant Breeding & Genetics,
School of Integrative Plant Science, Cornell University*

When Dr. Kass asked me to write a foreword for this volume, I was surprised; surely there were others in the maize community better suited? However, I can trace my scientific lineage as a maize geneticist directly to the community built by the *Maize Genetics Cooperation News Letter (MNL)*. I did my PhD at the University of Missouri in evolution and archaeology. However, while I was there, Drs. Ed Coe (editor of *MNL* from 1974-2000, after Emerson, and others) and Jim Birchler (*MNL* co-editor with Mary Polacco, now Schaeffer) introduced me to maize genetics. In 1993, I drove in a van to my first Maize Meeting with their graduate students. Every year since, I have attended the Maize Genetics meeting, where over 600 people of all ages come to discuss and work on the intricacies of maize. But, before jet setting around the US or planet was possible, and before the myriad of Internet communication's tools were available, the *Maize News Letter* was a visionary way to build an effective and collaborative community.

How did this community come about? As I look out the window of my office today, I see the building where, in 1932, the greatest geneticists from around the world gathered at Cornell University for The Sixth International Congress of Genetics. Despite the world being in the throes of the Great Depression, scientists traveled to Ithaca, New York to discuss the incredible breakthroughs occurring in genetics — the first Golden Age of genetics. At the time, the rediscovery of genetics was about 30 years old and if we look at the meeting attendees and talks, we can see the origins of many of the major branches of genetics represented for the first time. And, at that meeting, Dr. Rollins Emerson (1st *MNL* Editor) called together a side group of maize geneticists to develop a process to share knowledge and discovery across the community. This side meeting invigorated the previously established *Maize Genetics Cooperation News Letter*, which would, for the next decades, be the key catalyst for the community.

What other newsletter is a cooperation newsletter? This sense of cooperation was instrumental to the creation of our community, initially with sharing of information and genetics stocks. But over time, these founding geneticists and breeders collaborated with nearly every other field of science – physiology to archaeology to engineering. Cooperation evolved and added collaboration. Today, the breadth of science that is possible when working on maize through collaboration is what I love most about our science. Our community answers questions as precise as how a change in a single base of DNA affects the structure of the tassel to questions as overarching as how maize can play a sustainable role in feeding the world in the face of climate change. The newsletter let people know years before an official publication came out what various groups were working on. While there is always some competition for discovery, the community around the newsletter was dominated by cooperation and collaboration.

In this volume, Drs. Kass, Coe, and co-editors show how the *Maize News Letter* is central to the origins of maize genetics and community, and in no small part the origins of the entire modern genetics community. While I never had the honor of meeting Rollins Emerson, Barbara McClintock, George Beadle, or Marcus Rhoades, I have worked on questions that all of these people asked and even reanalyzed some of their data that was first reported in the *MNL*. In this volume, Lee Kass brings to life these founders of our scientific community, where we came from, and how our community was built. While this work highlights some scientific questions that remain open, the greatest lesson the *MNL* can teach us and future generations is how to build a community of learning and discovery, where the scientist, the science, and society all win.

PREFACE

Rollins A. Emerson, second Head of Cornell's Department of Plant Breeding, established the Maize Genetics Cooperation and the *Maize Genetics Cooperation News Letter (MNL)* at Cornell University (Kass et al. 2005, reprinted in this volume). It was published at Cornell from 1929 through 1955, and continued publication at The University of Illinois, Indiana University and The University of Missouri (Coe & Kass 2005, *MNL* 79; reprinted in this volume).

This 90th Anniversary book was inspired when in April of 2018 Kass searched the MaizeGDB online database (<https://www.maizegdb.org/mnl>) to locate a complete reference, including page numbers and author affiliations, for an article published in *MNL* 17, 1943. Coe, former *MNL* editor (1975-2000), helped locate the reference and confirmed that it was not possible to gain knowledge of affiliations for historical purposes without examining hard copies of the *MNL*. Many of those early *News Letters* had been retyped for the digital venue, and contributors' reports were not always shown in groups by affiliation (e.g., University, College, or other Institution), as can be found in the originals.

While searching for this reference, it occurred to Kass that Plant Breeding & Genetics at Cornell had Emerson's bound volumes of the earliest *MNLs* that were not in the Cornell Library. Before sending these *MNL* bound volumes (Vols. 2-14, 1932-1940; Vols. 15-21, 1941-1947, compiled by Emerson for the College of Agriculture Library) to the Cornell Archives, we desired to scan them "verbatim" and make them available in digital format. We also have a copy of what is now considered *MNL* Volume 1, 1929, Emerson, pp. 1-30. This was located among the papers of E.G. Anderson, at The University of Missouri, by Coe (*MNL* 53, Foreword, 1979). It was reprinted in a hard copy of *MNL* 53:117-130, March 1, 1979, "IV. 50 Years Ago," as part of the Historical Notes of the *MNL*, but was not initially available in digital format (see *MNL* archived volumes <https://www.maizegdb.org/mnl>; <https://mnl.maizegdb.org/mnl/53/>). A pdf version of *MNL* Volume 53 has since been added as a link: (<https://mnl.maizegdb.org/mnl/53/00MNL%2053or.pdf>). Volume 22 to date has been added as verbatim pdf versions by Coe and are posted at the online database, (<https://www.maizegdb.org/mnl>).

The early *MNL* articles were presented online, but were incomplete (available at Maize Newsletter Archives, <https://www.maizegdb.org/mnl>). Also, the early volumes (1-3) were mis-numbered on this website [the correct volume numbers were published by Coe and Kass (2005)]. The 1932 issue was listed as Volume 1, but the first Volume issued in 1929 was not included at this archive link (this volume was reprinted in *MNL* 53, as mentioned above). Considered to be the first *MNL* by Emerson, Volume 1, 1929 is correctly cited as *MNL* 1 at MaizeGDB, Reference Record, Emerson, R.A., 1929, *MNL* 1:1-30, "You who attended the "cornfab" in my hotel room ..." (https://maizegdb.org/data_center/reference?id=9020573). This web-link also reports that *MNL* 1 was reprinted in *MNL* 53. Biographical references for R.A. Emerson are included at: (<https://maizegdb.org/person?id=12877>).

Because the early *MNLs* were not available in digital format, we reached out to Robert Cooke, publisher of the Internet-First University Press, to ask if he might have an interest in publishing, as an e-book, Volumes 1-21 (1929-1947) of the *Maize Genetics Cooperation News Letter*, including the correspondence that accompanies these volumes. He was enthusiastic to publish the volumes if we could make arrangements to have them scanned. We were fortunate that Michael Cook of Albert R. Mann Library Digital Collections had the funding and resources for this endeavor, and he offered, in addition, to produce a Cornell eCommons webpage where the scans could also be viewed (see Introduction). Cook also suggested reprinting Coe & Kass (2005) in this volume for ease of comparison with original *MNL* volume numbers (see Appendix II).

We are, therefore, pleased to present here the early *MNLs* compiled by R.A. Emerson, with relevant photographs (see Introduction) and perspectives on its founding at Cornell University, 90 years ago this April.

Lee B. Kass
Edward H. Coe, Jr.
9 February 2019

ACKNOWLEDGMENTS

We acknowledge with thanks: the staff of Albert R. Mann Library for providing resources for scanning *Maize News Letters*; Jeffrey Piestrak, Digital Collections Specialist, for making the excellent scans; and Michael Cook, Head of Collections, for supervision. We also acknowledge Ed Buckler, Cornell University, for providing 1932 ICG photos; and Evan Earle, Director Cornell Archives and Peter Fraissinet, L.H. Bailey Hortorium, for identifying the building where the 1929 group photo was taken. Dr. Alexandra S. Kadner, WV medical writer and scientific consultant, provided assistance by alerting us to more recent cooperative-type Newsletters. We thank The Genetics Society of America for granting permission to reprint Kass et al. 2005, *Genetics* 169 (April 1): 1787-1797. We deeply appreciate Mark Sorrells, Professor of Plant Breeding & Genetics, for reviewing the manuscript. Hard copies of this volume were made available courtesy of School of Integrative Plant Science, Plant Breeding & Genetics Section. LBK thanks Plant Breeding & Genetics, Cornell University, and Plant & Soil Sciences, West Virginia University for logistical support. Special recognition is given to our publisher, J. Robert Cooke, for encouraging our efforts to make this project a reality.



Group photo of Sixth International Congress of Genetics, 24-31 August 1932, Ithaca, New York, taken outside northwest corner of the New York State Armory and Drill Hall (now Barton Hall), Cornell University Campus. (Courtesy of Edward S. Buckler) [For IDs see Jones (1932, Volume 1) or Crow (1992)]



[Left Half] Group photo of Sixth International Congress of Genetics, 24-31 August 1932, Ithaca, New York, taken outside northwest corner of the New York State Armory and Drill Hall (now Barton Hall), Cornell University Campus. (Courtesy of Edward S. Buckler) [For IDs see Jones (1932, Volume 1) or Crow (1992)]



[Right Half] Group photo of Sixth International Congress of Genetics, 24-31 August 1932, Ithaca, New York, taken outside northwest corner of the New York State Armory and Drill Hall (now Barton Hall), Cornell University Campus. (Courtesy of Edward S. Buckler) [For IDs see Jones (1932, Volume 1) or Crow (1992)]

INTRODUCTION

The *Maize Genetics Cooperation News Letter* (**MNL**) was founded by Rollins Adams Emerson (1873-1947) at Cornell University and has been published annually since 1929. It is a compendium of notes and information about on-going research intended to be shared throughout the maize research community. The *News Letters* were published by the Department of Plant Breeding at Cornell University until 1955. A partial name contraction to *News-letter* was made with Volume 64 in 1990. The publication became fully and only digital with Volume 88.

Emerson was head of Cornell's Department of Plant Breeding from 1914 to 1942 (Murphy & Kass 2007, 2011). He had been called from the University of Nebraska to succeed H.J. Webber, who established the Department at Cornell in 1907. Emerson and his students established a school of Maize Genetics and Cytogenetics, and in 1929 he founded the *Maize Genetics Cooperation News Letter*.

In this book we offer a full page verbatim scan of the first **MNL**, sent to maize cooperators by R.A. Emerson on 12 April 1929. The scan was made by Coe from the archived files of E.G. Anderson, who had spent his retirement years at the University of Missouri. Anderson had received his Ph.D. (1920) at Cornell with Emerson (Murphy & Kass 2007, 2011, pp. 24, 31, 33-34, 119).

As Emerson planned his retirement, he arranged to have all copies of the **MNL** bound for the College of Agriculture Library. Two bound volumes resulted (see back cover). When the new library (Albert R. Mann Library) was established, Emerson's bound volumes remained in the Department of Plant Breeding and eventually were passed along to Margaret Smith (see Kass et al. 2005). The back cover of this volume shows the two bound volumes of the early **MNLs** that were compiled for the library. Verbatim scans of these first bound volumes are also included here, and the originals will be deposited in the Cornell Archives for their History of Science Collections.

The first set of bound **MNLs**, which we located in the Department of Plant Breeding at Cornell (**MNL**, Vols. 2–14, 1932–1940), was numbered by hand in pencil, beginning with October 1932, labeled “Vol. 2.” (**MNL** 2; Coe & Kass 2005). The “Historical Notes on Maize Cooperation” listed on p. 56 of **MNL** 14 (1940) states that the mimeographed letter of April 12, 1929 is “considered *News Letter* 1.” The Cornell Plant Breeding Department's bound volumes appear to have been numbered retroactively under the guidance of Emerson, who was the secretary for **MNL**, Vol. 14, 1940. The binding on the first set of bound *News Letters* clearly shows that 1932 was considered to be **MNL** Vol. 2 (see image on back cover).

The **MNL** included unpublished data, unselfishly contributed by geneticists from many institutions (Murphy & Kass 2011, p. 23). This first and unique cooperative effort was so successful that it became widely copied. For example, the first volume of the *Drosophila Information Service* [**DIS**], issued in March 1934, mentioned the Emerson Cooperation and that *Drosophila* workers had planned to establish a similar service to that of the maize workers (Bridges & Demerec 1934, p. 2). Similar publications soon followed: *Mouse Genetics News* (Snell 1941, Law 1948), reestablished as *Mouse News Letter* (Dunn 1949); *Neurospora Newsletter* (1962-1985), later named *Fungal Genetics Newsletter* (1986-2007), and currently named *Fungal Genetics Reports* (2008-current); *Arabidopsis Information Service* (Röbbelen 1964-1973, Kranz 1974-1990), later The *Arabidopsis Information Resource* (**TAIR**); *Zebrafish Science Monitor* (1991-2000), which became *ZFIN NEWS* and then The *Zebrafish Information Network* (2004-current); *Worm Breeders Gazette* (**WBG**) (Edgar 1975-current); and a variety of other plant Newsletters that have come and gone, such as *Gramene* and The *Rice Genetics Newsletter* (1984-2007). See others as listed on the *Gramene* website (<http://archive.gramene.org/newsletters/newsletters.html>).

The first **MNL** (Vol. 1, 1929) was sent “To Students of Maize Genetics” in April of 1929, shortly after Emerson's “cornfab,” held in his hotel room at the AAAS Christmas meetings, December of 1928, in New York City (Kass et al. 2005). This mimeographed letter included a long folder of linkage information—linkage data, lists of genes, and “rainbow maps”—and the names of researchers assigned to nine of the ten linkage groups known at that time (see **MNL** 1, 1929, p. 2). Most of the researchers assigned to study the maize linkage groups were working at Cornell; the more familiar names were [George W.] Beadle, [Barbara] McClintock, [Allan C.] Fraser and of course R.A.

Emerson. Others working on linkage groups were affiliated with Bucknell University, Lewisburg, Pennsylvania; Iowa State University, Ames, Iowa; The University of Minnesota, St. Paul, Minnesota; Ohio Agricultural Experiment Station, Wooster, Ohio, in cooperation with the Office of Cereal and Crops Diseases, Bureau of Plant Industry, U. S. Dept. of Agriculture, Beltsville, Maryland; University of Wisconsin, Madison, Wisconsin; and Kansas State University, Manhattan, Kansas. Barbara McClintock shared the study of linkage group B-LG with Lewis J. Stadler of The University of Missouri, Columbia, Missouri.

Beadle would later share the 1958 Nobel Prize in Physiology or Medicine for "... discovery that genes act by regulating definite chemical events" (<https://www.nobelprize.org/prizes/medicine/1958/beadle/facts/>). McClintock, 1983 Nobel Laureate in Physiology or Medicine, was awarded an unshared prize for her "discovery of mobile genetic elements" (<https://www.nobelprize.org/prizes/medicine/1983/mcclintock/facts/>; Kass 2013ff.).

Ever honest and forthcoming, Emerson claimed "no credit" for assembling this first summary of data. Professor Fraser had "abstracted the available published papers" before leaving for a year in Europe, Emerson explained. Emerson also noted that his graduate student, "Mr. Beadle, has completed that work and assembled my own unpublished records and has arranged all the tables and charts" (Emerson, *MNL* 1, p. 1).

Supplementary communications were sent out by Beadle in November and December of 1929 and February of 1930. Emerson sent a 17-page mimeographed folder of revised maps on April 17, 1930, and in July 1930 he sent a second folder of linkage data that included 23 pages. The latter two communications were found in the papers of E.G. Anderson and at the Rockefeller Archives Center, respectively. They were identified by Emerson in his Historical Notes published in *MNL* 14:56, but were not included in the Plant Breeding Departments' bound volumes. These communications (not included here) were reprinted in *MNL* 54 (1980) and *MNL* 72 (1998), and are listed in Coe & Kass (2005).

The Maize Genetics Cooperation was formalized during the 1932 Sixth International Congress of Genetics held at Ithaca, NY (*MNL* 2, 1932), and was mentioned in Emerson's Historical Notes published in 1940 (*MNL* 14:56). Shortly before that conference, Emerson notified maize geneticists of his plan to establish a Cooperation of Maize Geneticists (ref. *MNL* 14:56; Coe & Kass 2005). Soon after the Congress, Emerson and his former student Marcus Rhoades issued what has been considered to be the first "*Maize Genetics Cooperation News Letter*" (October, 1932), in which unpublished data were freely shared among the members. Rhoades assumed editorship of the *MNL* after Emerson and George Beadle. Rhoades numbered the October 5th 1932 *MNL* as number 1, but as we have shown this had been identified by Emerson as *MNL* 2, 1932 (see scanned *MNL* Vol. 2 in this volume, and bound volume image on back cover; see also Kass et al. 2005, reprinted Appendix I; Coe & Kass 2005, reprinted Appendix II).

A group photograph taken at the 1932 Congress of Genetics is published in this Anniversary volume (before the Introduction). The photograph is slightly different from the one published in the Proceedings (Jones 1932, Vol. 1), given that Emerson's dog is included in the lower right corner. The scan was made from a photograph that was saved from the trash by Edward (Ed) Buckler, when he was affiliated with North Carolina State University (NCSU). We also have a similar photo in the Plant Breeding and Genetics files at Cornell. By examining the list of attendees at the Ithaca Congress (Jones 1932, Vol. 1, p. 25), we concluded that the framed photo that Buckler had saved from a storage closet at NCSU had been obtained by C.H. Bostian, who had joined the faculty at North Carolina State College, Raleigh, North Carolina (now NCSU) in 1930, and retired in 1973 (Bostian Wikipedia). He is identified by number 368, in the upper left side of the 1932 Ithaca Congress group photograph (see Crow 1992 or Jones 1932, Vol. 1). In addition, the President of the Ithaca Congress, T.H. Morgan, and R.A. Emerson, the General Chairman of the Local Committee, are seen in a photo (frontispiece) taken in Willard Straight Hall, the Headquarters of the Congress (Morgan 1932). This scanned image was also made from a photograph saved by Buckler. An image of the Executive Committee for the Congress, also from this NCSU collection, can be viewed on the eCommons webpage (*Maize Genetics Cooperation News Letter*, eCommons <https://ecommons.cornell.edu/handle/1813/58745>).

At the 1932 International Genetics Congress, Emerson gave an opening address titled “The Present Status of Maize Genetics” (Kass & Bonneuil 2004). In his introduction he declared:

“I cannot refrain from noting here a very real advantage experienced by students of maize genetics ... I am aware of no other group of investigators who have so freely shared with each other not only their materials but even their unpublished data. The present status of maize genetics, whatever of noteworthy significance it presents, is largely to be credited to this somewhat unique, unselfishly cooperative spirit of the considerable group of students of maize genetics. In this connection I want gratefully to acknowledge the help of many persons who have contributed directly or indirectly to this summary statement of the status of maize genetics” (Kass 2001, Kass et al. 2005).

By October 1932, *MNL* 2 (= Rhoades *MNL* 1) was issued from Cornell, and provides a record that ten linkage groups had been assigned to ten maize workers. A report of the meeting held at the International Congress of Genetics was included in this *MNL*, as recorded by Secretary Rhoades (see also Kass et al. 2005). Emerson’s numbered *MNL* 3, January 23, 1933, 16 pages (= Rhoades *MNL* 2), is identified as the “Third Corn News Letter” (*MNL* 14:56), and provided a long list of known genes of maize, among other items. By November 13, 1933, Rhoades issued a two-page call for information anticipating the forthcoming *MNL* 4, published the following month. This November call is not included in the Emerson bound volume, but was included in the files at Missouri (Coe & Kass 2005). By December 1933, Emerson’s and Rhoades’ *MNLs* were both numbered in agreement as *MNL* 4, 7 pages. Thereafter, the *MNL* volume numbers correspond (Coe & Kass 2005).

Rhoades left Cornell in 1935 and Emerson assumed editorship once again. In 1937, Derald Langham, Emerson’s graduate student (Ph.D. 1939), became editor through *MNL* Volume 13 (March 1939). Emerson re-assumed editorship through 1944 (*MNL* 18), with the exception of *MNL* 15 (April 1, 1941), edited by Professor Fraser. Fraser had planned to assume editorship but, sadly, died in September of 1941. Robert L. Cushing was hired in 1943 to replace Fraser. Cushing edited *MNLs* 19 and 20 (1945-1946) and was succeeded by Harold H. Smith as editor and Professor of Genetics through *MNL* 26 (1952). It may have been Smith, in consultation with Emerson, who had the second set of *MNLs* (Volumes 15-21) bound for the library.

We have also included scans of the Cornell Plant Breeding Department’s second bound volume of *Maize News Letters* (*MNL* 15-21, 1941-1947; see image on back cover). We believe that Emerson may have compiled this bound volume prior to his death on 8 December 1947. Note that *MNL* Volume 21, which we include in this book, was not scanned from this second bound volume. Due to technical difficulties with the library’s book scanner, *MNL* Volume 21 was scanned from an unbound identical Albert R. Mann Library copy instead. As mentioned in the Preface, Cook provided funds to scan these early maize volumes, and provided guidance on copyright, and other items of value to include for historical perspective.

Professor Margaret Smith (Cornell Ph.D. 1982) has held Cornell’s bound *MNL* collection for many years (Kass et al. 2005). She joined the Plant Breeding faculty in 1987. R.P. Murphy (Murph), former Chair of Plant Breeding (1953-1964), introduced Kass to Smith, when Kass sought information about McClintock’s affiliation with the *Maize Genetics Cooperation News Letter* at the encouragement of former editor Coe (see Kass 2013ff.). Although Murphy had long ago left maize research, he had done his Ph.D. at Minnesota with one of the most prominent maize geneticists of his generation, Herbert K. Hayes, and continued his interest in the subject through the faculty in Plant Breeding (Murphy & Kass 2007, 2011). Having access to the early maize volumes led to cooperative efforts to expand the chronological list of materials related to maize cooperation (Coe & Kass 2005) and to provide historical perspectives on the cooperative spirit fostered at Cornell by Emerson (Coe 2001, Kass et al. 2005). Smith also tutored Kass in the reproductive biology of maize to further her understanding of the extensive field work required, and she introduced Kass to the cytogeneticists teaching in the Plant Breeding Department, who used slides prepared by McClintock for work reported in *MNL* (see Kass 2013ff.).

Judy Singer has been an invaluable resource to this project, and has been a long time member of Cornell’s Department of Plant Breeding and Genetics. Singer facilitated all contacts for obtaining the photographs that appear in this book, and she designed and took the photo that appears on the back cover. Singer’s cooperative spirit is reminiscent of the manner fostered by Plant Breeding Department Head Rollins A. Emerson. For many years, she has

worked towards the preservation of historical documents in this historically notable department, initiated by Dean Liberty Hyde Bailey in 1907 (Murphy & Kass 2007). Murphy, Kass, and Singer worked closely to save and identify documents for the history of Cornell's Plant Breeding Department (Murphy & Kass 2007), which was subsumed into the School of Integrative Plant Science when it was established in 2014, and to deposit these documents for posterity in the Cornell Archives.

In this tradition, and in celebration of the 90th Anniversary of the *Maize Genetics Cooperation News Letters*, the editors of this volume are pleased to present a digital record of the early *Maize News Letters*, founded at Cornell University by R.A. Emerson in April of 1929.

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Introduction to *Maize Genetics Cooperation News Letters* Volumes 15-21 (1941-1947)

The following pages offer verbatim scans of the second set of bound *MNL* Volumes 15-21 (1941-1947) beginning with *News Letter* 15, April 1, 1941, and including Fraser's call of January 1, 1941. The appreciation that preceded page 1, and is listed in Coe & Kass (2005), is not included in this second bound Volume (it may be viewed at the following link <https://mnl.maizgdb.org/mnl/15/02Fraser.htm>). The binding on this second set of *News Letters* begins with Vol. 15 (see image on back cover; see also Kass et al. 2005, Appendix I and Coe & Kass 2005, Appendix II).

MNL Volumes 15-21 are arranged below sequentially, and interleaved with calls and other items as found in the Plant Breeding bound volumes (scanning of *MNL* bound volumes was arranged by Michael Cook).

On Emerson's recommendation, Allan C. Fraser assumed Editorship of the *MNL* as of April 1, 1941 but, sadly, died in September of 1941. Succeeding editors through 1947 were R.A. Emerson, Robert L. Cushing, and Harold H. Smith (Coe & Kass 2005, Appendix II). It may have been Smith, in consultation with Emerson, who had the second set of *MNLs* (Volumes 15-21) bound for the Cornell Agriculture library.

MAIZE GENETICS COOPERATION

NEWS LETTER

15

8-21
April 1, 1941

LIBRARY
NEW YORK STATE
COLLEGE OF AGRICULTURE

The data presented here are not to be used in
publications without the consent of the authors.

Department of Plant Breeding
Cornell University
Ithaca, N. Y.

MAIZE GENETICS COÖPERATION
DEPARTMENT OF PLANT BREEDING
CORNELL UNIVERSITY
ITHACA, NEW YORK

January 21, 1941

To Maize Geneticists:-

The call for material for the 1941 issue of the Maize News Letter has been delayed this year much longer than usual. This was the result of considerable uncertainty as to the source of support for the Maize Genetics Cooperation. While we can make no positive statements now, it seems likely that continued support of the Maize Cooperation at Cornell will be forthcoming from some quarter.

Items submitted for the 1941 News Letter should include new linkage data, descriptions of new characters, suggestions on breeding and cytological technique, and all similar material likely to be of general interest, and valuable to have on record.

We plan to print in the News Letter references to all important maize publications since our last issue. It will help to make this list more complete if you will send us the titles of papers in press, with the names of the journals which have accepted them.

The dead line on contributions is March 1, 1941. May we have your contribution soon?

Sincerely yours,

A. C. Fraser

A. C. Fraser
Secretary

ACF:P

MAIZE GENETICS COÖPERATION
DEPARTMENT OF PLANT BREEDING
CORNELL UNIVERSITY
ITHACA, NEW YORK

-1-

April 1, 1941

To Maize Geneticists:-

At the request of Professor Emerson, I am taking over the job of Secretary of the Maize Genetics Cooperation. It is hoped that this arrangement will give continuity to the work of maintaining stocks and will enable us better to plan ahead.

Actually most of the detailed work with the stocks is at present in the hands of James E. Welch, one of our graduate students from Honolulu. Welch has a Ph.D. major problem on corn. He has made all of the pollinations of the "co-op" material this past summer and has proved very helpful in other ways.

You will be glad to learn that the Rockefeller Foundation has made a grant to Cornell University to cover the cooperative work with the maize stocks for three years, starting February 1, 1941. The Foundation has further indicated its willingness to consider a request for the renewal of the grant at the end of this period.

A. C. Fraser

Contents of the News Letter

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II.	Editorial Policy of Genetics	Page 3
III.	General News Items	Page 4
IV.	Miscellaneous Co-op Items	Page 49
V.	Maize Publications	Page 50
VI.	New Genes	Page 56
VII.	Maps	Pages 28 & 35.

II. Editorial Policy of GENETICS

It will doubtless interest maize geneticists to know the editorial policy of GENETICS concerning the symbolizing of genes, linkage groups and chromosomes of maize. The present policy has been in use for sometime and seems to be satisfactory.

Arabic numerals are used to designate both linkage groups and chromosomes.

Literal superscripts are used to represent different members of an allelic series.

No subscripts are used to represent different genes which give similar phenotypes. The numeral shall be raised to the same level as the rest of the symbol, i.e. v³ and not v₃. The first member of such a series shall be designated only by the literal symbol without the accompanying numeral "one" e.g. bm¹ and a¹ shall be simply bm and a. This will prevent the confusion which would result from such symbols as a and a¹ if the numeral "one" was used with a but not as a subscript.

All gene symbols are italicized but the symbols T, Df and In representing translocations, deficiencies and inversions, respectively, are not italicized.

M. M. Rhoades

III. General News Items

California Institute of Technology,
Pasadena, California

1. Cherry pericarp - An allele of R has been found in Pueblo Indian maize in which cherry pericarp color is associated with colored aleurone (i.e. R^{ch}). It has been tested in back crosses to r-tester.
2. Long inversion on chromosome 2 - The inversion is well out toward the end of each arm, thus inverting four-fifths or more of the chromosome. Tests place the left break between gl2 and B, the right break far beyond v4 but in the v4-ch interval. In the homozygous inversion the map order is lg-gl2-v4-B-ch. Data on map distances are as follows:

	<u>Total</u>	<u>Crossovers</u>	<u>Percent</u>
lg-v4	851	321	37.7
gl2-v4	828	303	36.6
v4-B	2425	1006	41.5
B-ch	1205	300	24.9

3. Position of ba2 - A backcross culture homozygous for the long inversion but heterozygous for B, ba2 and v4 suggest that ba2 lies between B and v4. The data are

<u>B</u>	<u>v4</u>	<u>0</u>	<u>1</u>	<u>2</u>	<u>1.2</u>
<u>ba2</u>		36 36	29 16	5 10	5 5

E. G. Anderson

Columbia University, New York City

1. Additional data on the location of Dt.
In the News Letter of March 5, 1940, backcross linkage data for Dt and Wx and F₂ data for Dt and Sh were given. These data showed 41 percent recombination between Dt and Wx and 27 percent between Dt and Sh. The order apparently was Dt Sh Wx and the recombination value with Sh indicated that Dt should fall close to Yg2 near the end of the short arm of chromosome 9. The following data on the location of Dt were obtained this past year.

<u>Dt Sh</u>	x	dt sh	gave	<u>Dt Sh</u>	<u>Dt sh</u>	<u>dt Sh</u>	<u>dt sh</u>	<u>Total</u>
dt sh				617	266	305	588	1776

Dt Sh - 32 percent recombination

	$\frac{Dt}{dt}$	$\frac{Yg}{yg}$	$\frac{Wx}{wx}$	selfed
Dt Yg Wx - 1450				dt yg Wx - 385
Dt yg wx - 38				dt Yg Wx - 223
Dt Yg wx - 360				dt Yg wx - 63
Dt yg Wx - 36				dt yg wx - 238

Total 2793

Recombination values: Dt Yg 11 %
Dt Wx 42 %
Yg Wx 37 %

	$\frac{Dt}{dt}$	$\frac{Yg}{yg}$	$\frac{Sh}{sh}$	$\frac{Wx}{wx}$	selfed	
Dt Yg Sh Wx - 387					dt Yg Sh Wx - 52	Total : 779
Dt yg Sh Wx - 7					dt yg Sh Wx - 84	
Dt Yg Sh wx - 59					dt Yg sh Wx - 2	Recombination values:
Dt yg Sh wx - 2					dt yg sh Wx - 49	Dt Yg 10 %
Dt Yg sh wx - 35					dt Yg Sh wx - 1	Dt Sh 27 %
Dt yg sh wx - 10					dt yg Sh wx - 3	Dt Wx 44 %
Dt Yg sh Wx - 15					dt Yg sh wx - 9	Yg Sh 24 %
Dt yg sh Wx - 3					dt yg sh wx - 61	Yg Wx 38 %
						Sh Wx 20 %

These data indicate that the order is Dt Yg Sh Wx and they place Dt ten units beyond Yg. Creighton found only one percent recombination between Yg and the terminal knob on the short arm of 9 so there is some discrepancy here. It should be noted that in selfing a Dt dt plant three classes of seed are obtained, i.e. the Dt Dt Dt, the Dt Dt dt and the Dt dt dt classes. In this latter class possessing a single Dt allele the mutation rate is so low that a considerable number of Dt dt dt seeds were classified as dt because no dots (mutations) are evident. This fact introduces some error into the recombination values but nevertheless the order should be as indicated. The locus of Dt therefore lies beyond Yg and must be very near the end of the short arm of chromosome 9.

2. Mutation of a to different alleles.

Four alleles at the a locus have been described by Emerson and Anderson. These four are a, a^p, A and A^b. Only a has its mutation rate increased by Dt. Mutation of a to five different alleles has occurred in a Dt stocks. One of the five is a mutation to an allele similar to a in its effect on aleurone, plant and pericarp color but differs in that it is stable with Dt. This allele has been found several times. It is of some interest that these so-called stable alleles are not completely stable with Dt; an occasional dot is found in the aleurone (about .4 dot per seed in Dt Dt Dt seed) but these dots are commonly much smaller than normally is the case indicating that the mutations when they do occur take place at a relatively late stage.

A second allele is one identical in all respects with A. Out of twenty mutations tested, which give deep aleurone color and purple plant color with B Pl, eighteen of them were to A.

A third allele was found in the group of twenty mutations mentioned above. This allele produces deep aleurone and purple plant color but gives a recessive brown pericarp color with P. This is a new allele.

A fourth allele is one like A in its effect on aleurone and plant color but produces a red-brown pericarp color that is recessive to the red color produced by A but is dominant to the recessive brown of a. This is a new, previously undescribed allele.

The fifth allele found is one resembling a^p in its effect on aleurone and plant color but giving a recessive brown pericarp color instead of the dominant brown produced by a^p. This is also a new allele.

The data on hand indicate that mutations of a to different alleles do not occur with equal frequencies. Although four new alleles have already been found it may be expected that additional new ones will appear as these experiments are continued.

No effect of Dt on any locus other than a has been found. This is true for the unstable pericarp allele (P^{vv}) as reported before and also for the unstable waxy allele.

3. Further studies on the behavior of the abnormal tenth chromosome. (See last News Letter)

Plants heterozygous for a normal chromosome 10 and an abnormal chromosome 10, differing from the normal in that it has a piece of chromatin attached to the distal end of the long arm as described by Longley (1937, 1938), give an unusual type of behavior for these two homologues. When used as the female parent the percentage of the basal megaspores receiving the abnormal chromosome 10 is approximately 67 percent instead of the expected 50 percent. The R locus was found to lie extremely close to the end of the short arm; there being one percent of recombination between R and the distal end of the short arm. This placing of R would mean that d7 does not lie beyond R as Singh's data indicated. Crossover studies in the g R region showed no reduction in plants heterozygous for the abnormal chromosome so it is likely that the low recombination value between R and the end is the true distance and is not due to a reduction from the true value caused by the presence of the redundant piece of chromatin. Earlier, it was suggested that competition among megaspores might account for the excess number of eggs carrying the abnormal chromosome 10, i.e. in a considerable number of cases non-basal megaspores with the abnormal chromosome would develop into the embryo sac at the expense of basal megaspores with normal chromosomes 10. Examination of 200 young embryo sacs showed, however, that the embryo sac always arose from the basal megaspore so the above hypothesis can be definitely ruled out. The alternative explanation is that selective segregation during the two meiotic divisions results in the abnormal chromosome passing to the basal megaspore more frequently than expected on a random basis. This explanation is being tentatively accepted. There is no sterility on the ears so abortion of ovules with the normal chromosome 10 does not account for the discrepancy. Since the R locus is so close to the end of the long arm it may be used to mark the normal and abnormal chromosomes thus making it possible to collect a large amount of data. When pollen from a plant heterozygous for the two chromosome types is used it is found that pollen carrying the abnormal chromosome is at a disadvantage when competing with grains carrying the normal chromosome. Using the R alleles to mark the two chromosomes it was found in one experiment that 59.7 of the functioning pollen grains carried the normal chromosome. Since comparable results were obtained when different normal chromosomes 10 were used against the abnormal chromosome 10 it may be argued that the redundant piece of chromatin is not wholly inert but possesses some genetically active material.

If selective segregation is the correct explanation of the unusual results obtained on the female side it is of some interest to give the following results. In the summer of 1939, 75.7 percent of the individuals in a

population of 4,501 coming from female plants heterozygous for the two chromosome types carried the abnormal chromosome 10. A duplicate of the seed planted in 1939 was planted in 1940 but only 62.8 percent of the individuals in a population of 4,922 possessed the abnormal chromosome. Since the two lots of seed were identical it appears that environmental conditions influence the segregation of the heteromorphic bivalent. This behavior is similar to that found in certain insects where temperature differences determine whether the X or Y chromosome is extruded into the polar bodies.

4. Singleton found a marked effect of the female parent on the functioning of sp1 pollen. Tests were made using four different r-testers to determine if a similar situation existed for sp2. The data obtained show no indication of an effect of these female parents on the functioning of sp2 pollen.
5. Jenkins gave the writer a selfed stock homozygous for mottled aleurone. He had found it extremely difficult to get a homozygous stock in which all seeds showed mottling since the mottled condition is extremely susceptible to the action of modifiers. This strain was turned over to the writer because it seemed possible that this case was similar to the a-Dt situation where one gene stimulates the mutability of another. The mottling proved to be caused by an r allele and was not due to another gene causing r to mutate. This allele is a new member of the R series. The mottled condition resembles most closely that produced by a single dose of R. It is not the same as the marbled and stippled alleles found in certain strains from Mexico and South America.

M. M. Rhoades

Connecticut Agricultural Experiment Station,
New Haven, Connecticut

1. The "miniature seed" gene which markedly reduces the amount of tissue in the endosperm and embryo has no effect upon pollen tube growth and little or none upon plant growth. This is additional clear evidence that nuclear factors have a particular time for their action and are specific for certain tissues.
2. Wire stapling pliers are being used by many corn breeders to fasten paper bags on tassels and ear shoots in place of wire clips. The stapled bags are more secure and take less time to put on. The cost of the staples is about the same as for paper clips but more have to be used. (Stapler and staples made by Neva-Clog Products, Inc., Bridgeport, Conn.)

D. F. Jones

1. The mottling factor was given the symbol Mt in the Cornell Memoir 180. We have tested several stocks for mottling and have found all except one, C626 purple flint, to produce mottling in seeds of the constitution r r R. However C626 suppresses mottling when the pollen is applied to any r r stock. Hence, it seems to us that mottling is the recessive condition and no-mottling dominant. In 1940 evidence that the mottling factor mt and r are allelic, was obtained. The inbred C78 A C r pr mt (mottling) had been crossed by C626 A C R Pr Mt (no mottling). The F₁ hybrid was selfed and also pollen was applied to a r mt stock. One ear backcrossed gave 120 colored (none mottled) and 133 colorless. Three selfed ears gave 825 colored (no mottled kernels) to 268 colorless. Although these data are fragmentary they indicate that R and Mt are allelic or very closely linked, much closer than the 12% of crossing over originally calculated by Kempton. Further evidence will be obtained in 1941. I should be glad to receive additional stocks of A C R that are known not to produce mottling.
2. Status of Connecticut Sweet Corn Hybrids. Possibly the maize geneticists will be interested in an item regarding the practical phase of genetics. Sweet corn hybrids developed by the Connecticut Experiment Station are increasing in use each year. In 1940 approximately 500,000 pounds of seed were produced. This amount is sufficient to plant 50,000 acres or 10% of the total sweet corn acreage in the country. More than 95% of this production had C13 as one parent. This is an early inbred almost immune to bacterial wilt. The use of this inbred in the early hybrids has practically solved the bacterial wilt problem for early corn. This inbred was first distributed in 1936, 73 pounds being sold. Four years later it was used in the production of approximately 475,000 pounds of seed. The three principal hybrids comprising this inbred are Spancross (C4.13), Marcross (C6.13) and Carmelcross (P39. C13). Considerably more seed will be produced in 1941 as well as seed of three new hybrids, C23.P39, C27.P39, and C15 x C13. A letter of March 3 from one of the leading producers of hybrid sweet corn seed states that now Marcross (C6.13) is second to Golden Cross Bantam in poundage, and that all open pollinated varieties are falling off rapidly. Hybrid corn is one of the best examples of the contribution of Genetics to practical agriculture.

W. R. Singleton

1. Endosperm divisions have been examined further for determining types of aberrant mitoses in lines showing high rates of mosaic formation on the mature kernel. Evidence for a relation between aberrant chromosome

divisions and observed genetic changes was obtained from control pollinations. The female parent was the same in both crosses. The resulting seed of one cross gives a high frequency of variegation, whereas from the other pollen parent there are very few or no mosaics observed. Cytological study of the endosperm divisions from both pollinations (10-12 days after pollination) showed a mean difference in percent of aberrant divisions of 3.24 (3431 divisions observed. $P = .01-.05$). This is a highly significant difference although many of the aberrant divisions are probably associated with changes that would not be observed genetically.

F. J. Clark

Cornell University, Ithaca, N. Y.

I am indebted to Dr. M. J. Murray for indispensable help in making the records to be reported here.

1. The order of br f - as noted in the News Letter of 1940, page 17, Bryan (News Letter 1938, page 5) had questioned the published order of the genes br and f. My report of last year was not wholly satisfactory because I was obliged to limit it to plants recorded as f. The records reported here were made last summer and are taken mostly from 5-point tests involving br f an and, in addition, gs or bm2 and another chromosome-1 gene or translocation. They are assembled here for more ready reference as 3-point tests (items 1 and 2 below)

Regions						
<u>Item</u>	<u>Genes</u>	<u>0</u>	<u>1</u>	<u>2</u>	<u>1-2</u>	<u>Total</u>
1	br f an	512-376 888	26-25 51 4.4%	78-125 203 17.5%	12-3 15 1.3%	1157
2	br f an	1109-853 1962	26-44 70 3.2%	92-73 165 7.5%	7-2 9 0.4%	2206

<u>Item</u>	<u>Genes</u>	<u>0</u>	<u>1</u>	<u>2</u>	<u>1-2</u>	<u>Total</u>	<u>Reference</u>
3	br f an	347	22 4.8%	77 17.0%	7 1.6%	453	N.L. '40, p.17
4	br f an	760	40 4.2%	156 16.3%	4 0.4%	960	L.S. '35, p.35
<u>Total</u> 1-4	br f an	3957	183 3.8%	601 12.6%	35 0.7%	4776	
5	br f ad	975	47 4.0%	141 12.1%	3 0.3%	1166	L.S. '35, p.35
6	as br f	263	93 24.7%	21 5.6%	0	377	L.S. '35, p.35
7	br f Kn	446	21 3.3%	148 23.1%	25 3.9%	640	N.L. '38, p. 5

Item 2 (above) includes cultures involving translocations which apparently reduced crossing over. Both lots indicate the order to be br f an. Results reported in last year's News Letter (item 3) and various records published in the Linkage Summary (items 4-6) are included for comparison. The locus of ad is very near that of an and, therefore, to the right of br as is Kn also, while as is certainly to the left of br. Bryan's records are repeated in item 7.

It is obvious from these records that, in my material, f is to the right of br. Bryan's records do not agree with mine, but they are not wholly conclusive, because, on the assumption of either order of br f, the double crossovers are so nearly equal to the single crossovers in the short region.

Loci of chromosome-1 translocations. Further tests of the linkage relations of several chromosome-1 translocations have been made. The genes included in these tests are br f an and either gs or bm2.

These records indicate that Tl-6a, Tl-10a, Tl-7b and Tl-7c are to the left of br in the order given here with Tl-6a relatively far from br and Tl-7c relatively near it. Tl-5a appears to be very near to and to the right of f, between it and an. Tl-3d and Tl-4 are between an and gs and relatively near an. Crossing over percentages between these several translocations and br, as reported here, are,

For the most part, in close accord with those reported by Anderson (N. L. 1938, p. 6). Agreement is good also between the placements reported here and Anderson's cytological observations, except for Tl-7c.

Five-point Translocation Tests

Region	Tl-6a : +		Tl-10a : +		Tl-10a : +		Tl-7b : +		Tl-7b : +	
	+ : br		+ : br		+ : br		+ : br		+ : br	
	+ : f		+ : f		+ : f		+ : f		+ : f	
	+ : an		+ : an		+ : an		+ : an		+ : an	
	+ : bm2		+ : gs		+ : bm2		+ : gs		+ : bm2	
0	137		118		73		93		110	
1	30		5		8		4		3	
2	5		2		1		4			
3	34		14		18		3		7	
4	101		55		52		17		59	
1-2	1									
1-3	1		2		5		2			
1-4	17		5							
2-3	2		1		2					
2-4	6		1		10		1			
3-4	17		1		1		1			
1-2-3	1		2		1					
1-2-4							1			
1-3-4			1							
2-3-4										
1-2-3-4	—		—		—		—		—	
Total	352		207		171		126		179	
Percent recom- bina- tion	T-br	14.2	T-br	7.2	T-br	8.8	T-br	5.6	T-br	1.7
	T-f	17.3	T-f	8.2	T-f	9.4	T-f	8.7	T-f	1.7
	T-an	31.2	T-an	13.5	T-an	26.3	T-an	10.3	T-an	5.6
	T-bm2	48.4	T-gs	38.2	T-bm2	47.4	T-gs	23.0	T-bm2	38.5
	br-f	4.2	br-f	2.9	br-f	0.3	br-f	4.8	br-f	0
	br-an	17.9	br-an	10.1	br-an	18.7	br-an	9.5	br-an	3.9
	br-bm2	45.1	br-gs	37.7	br-bm2	44.5	br-gs	20.6	br-bm2	36.9
	f-an	14.5	f-an	10.1	f-an	17.0	f-an	4.8	f-an	3.9
	f-bm2	46.2	f-gs	38.7	f-bm2	46.2	f-gs	19.1	f-bm2	36.9
	an-bm2	39.9	an-gs	30.4	an-bm2	40.8	an-gs	15.9	an-bm2	33.0

	Tl-7c	:	+	+	:	br	+	:	br	+	:	br	+	:	br
	+	:	br	+	:	f	+	:	f	+	:	f	+	:	f
Region	+	:	f	Tl-5a	:	+	+	:	an	+	:	an	+	:	an
	+	:	an	+	:	an	Tl-3d	:	+	Tl-3d	:	+	Tl-4	:	+
	+	:	gs	+	:	bm2	+	:	gs	+	:	bm2	+	:	bm2

0	160	142	119	59	185
1	1	5	5	2	4
2	9	6	4	4	4
3	4		1		4
4	20	72	9	36	125
1-2	3				
1-3		1			
1-4	6	5	1	1	3
2-3		1			1
2-4	2	3	1	1	3
3-4	1	2	1	2	8
1-2-3	1				
1-2-4					
1-3-4					1
2-3-4				1	
1-2-3-4					
Total	207	237	141	106	338

	T-br	2.9	br-f	8.8	br-f	4.2	br-f	2.8	br-f	2.4
	T-f	6.3	br-T	9.4	br-an	7.8	br-an	8.5	br-an	3.6
Percent	T-an	12.6	br-an	26.3	br-T	9.2	br-T	9.4	br-T	7.7
recom-	T-gs	16.9	br-bm2	47.4	br-gs	13.4	br-bm2	40.6	br-bm2	40.5
bina-	br-f	6.3	f-T	0.3	f-an	3.5	f-an	5.7	f-an	2.4
tion	br-an	10.6	f-an	18.7	f-T	4.9	f-T	6.6	f-T	5.9
	br-gs	17.9	f-bm2	44.5	f-gs	17.6	f-bm2	39.6	f-bm2	40.4
	f-an	5.8	T-an	17.0	an-T	1.4	an-T	2.8	an-T	4.1
	f-gs	14.5	T-bm2	46.2	an-gs	8.5	an-bm2	35.8	an-bm2	40.2
	an-gs	15.0	an-bm2	40.8	T-gs	8.5	T-bm2	38.7	T-bm2	41.4

3. Tassel-seed 3 and tassel-seed 6 - The results of tests reported in the 1940 News Letter by Lindstrom (p. 25) and by me (p. 16) suggest that Ts3 is between an and gs, while Ts6 is near bm2 and probably to the right. The records reported by Lindstrom, tho conclusive in showing that Ts6 is near bm2, are inconclusive with respect to whether Ts6 is to the right or the left of bm2. Where one region is as long as that between br and bm2 and the other as short as bm2 to Ts6, double crossovers are apt to be as frequent as are singles in the short region. My last year's records, involving an and either gs or bm2 are unsatisfactory because of the wide differences between complementary classes of crossovers. The records

presented here are equally unsatisfactory for the same reason. They are given first in a table as 4- and 5-point tests with complementary crossover classes combined.

Four- and five-point tests with Ts3 and Ts6

Regions	+ : br		+ : br		+ : br		+ : br		+ : br		+ : an	
	+ : f		+ : f		+ : f		+ : f		+ : f		+ : gs	
	+ : an		+ : an		+ : an		+ : an		+ : an		Ts6 : +	
	Ts3 : +		Ts3 : +		Ts3 : +		+ : gs		Ts6 : +		+ : bm2	
	+ : gs		+ : bm2				Ts6 : +		+ : bm2			
0	88		68		104		82		26		152	
1	4		7		11		6		2		56	
2	21		15		22		32		12		35	
3	21		14		19		35		22		11	
4	33		30				31		1			
1-2					4		1		1		16	
1-3					1		5				1	
1-4			2				2					
2-3					5		3		3			
2-4	3		9				16					
3-4	16		5				19					
1-2-3					4							
1-2-4							1					
1-3-4							1					
2-3-4	2		1				1					
1-2-3-4	—		—		—		—		—		—	
Total	188		151		170		235		67		271	

Percent Recombination

br-f	2.1	br-f	5.9	br-f	11.9	br-f	6.8	br-f	4.5	an-gs	26.9
br-an	16.0	br-an	22.5	br-an	22.9	br-an	28.1	br-an	25.4	an-Ts6	33.6
br-Ts3	34.6	br-Ts3	34.4	br-Ts3	33.0	br-gs	46.8	br-Ts6	53.7	an-bm2	38.0
br-gs	42.0	br-bm2	44.4	f-an	20.6	br-Ts6	45.5	br-bm2	55.2	gs-Ts6	19.2
f-an	13.9	f-an	16.6	f-Ts3	27.1	f-an	23.0	f-an	23.9	gs-bm2	22.9
f-Ts3	32.5	f-Ts3	28.5	an-Ts3	17.1	f-gs	46.8	f-Ts6	52.2	Ts6-bm2	4.4
f-gs	41.0	f-bm2	41.1			f-Ts6	45.5	f-bm2	53.7		
an-Ts3	20.8	an-Ts3	13.3			an-gs	27.2	an-Ts6	37.3		
an-gs	30.3	an-bm2	36.5			an-Ts6	39.6	an-bm2	38.8		
Ts3-gs	28.7	Ts3-bm2	31.2			gs-Ts6	30.2	bm2-Ts6	1.5		

The data, as presented in the accompanying table indicate that Ts3 is between an and gs, and Ts6 near bm2 and to its left. The unsatisfactory nature of the data is well shown when arranged as 2-point tests involving an and either Ts3 or Ts6, as follows:

$\frac{+ \text{ Ts3}}{\text{an} \quad +}$	+Ts3	++	anTs3	an+	Total
	64	39	0	85	188
	56	16	4	75	151
	<u>63</u>	<u>25</u>	<u>4</u>	<u>78</u>	<u>170</u>
Total	183	80	8	238	509

Total Ts3 = 191, non-Ts3 = 318
 " an = 246, non-an = 263

$\frac{+ \text{ Ts6}}{\text{an} \quad +}$	+Ts6	++	anTs6	an+	Total
	77	80	13	65	235
	24	16	9	18	67
	<u>112</u>	<u>63</u>	<u>28</u>	<u>68</u>	<u>271</u>
Total	213	159	50	151	573

Total Ts6 = 263, non-Ts6 = 310
 " an = 201, non-an = 372

In the cultures involving Ts6, an was strikingly and Ts6 somewhat deficient. In the Ts3 cultures, an was slightly and Ts3 decidedly deficient. The striking feature of these records, however, is the discrepancy between complementary crossover classes, ++ to an Ts6 being over 3 to 1 and ++ to an Ts3 10 to 1.

It seems likely that some, perhaps many, plants recorded as +Ts6 may have been an Ts6. The tassels were not removed and in many cases, ears failed to develop, and it is difficult to determine an from the tassels alone of Ts6 plants. With Ts3 and an, experience of some years has led me to question whether there may be an inhibiting effect such that, when heterozygous Ts3 and homozygous an are together, both characters generally fail to develop. But no adequate test of such a notion has been attempted.

4. The locus of vestigial - A 5-point test of Vg with br f an bm2 has given the following results from the F₁ genotype

$\frac{+ \text{ Vg} \quad + \quad +}{\text{br} \quad + \quad \text{f an} \quad \text{bm2}}$

<u>0</u>	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>1-3</u>	<u>1-4</u>	<u>2-4</u>	<u>3-4</u>	<u>Total</u>
164	5	1	42	103	4	2	1	15	337

Per cents of recombination are as follows:

br-Vg 3.3, br-f 3.9, br-an 19.6, br-bm2 44.8, Vg-f 0.6,
Vg-an 18.4, Vg-bm2 44.8, f-an 18.1, f-bm2 45.1, an-bm2 35.9.

Sprague (Jour. Heredity 30: 143-145, 1939) has shown that Vg is between br and f, a locus supported by the data presented here. I cannot, however, agree with his suggested order of f Vg br bm2. His three-point test, involving a very short region with a very long one, is unsatisfactory as pointed out by him, but the data as reported suggest the order br Vg bm2. His four-point test, again involving a very long region with very short ones, as a whole indicates the order suggested by him, but, when bm2 is disregarded, the resulting three-point data are:

$\frac{+ \text{ Vg } +}{\text{br } + \text{ f}}$	<u>0</u>	<u>1</u>	<u>2</u>	<u>1-2</u>	<u>Total</u>
	53	2	6	0	61

These data, obviously, afford no evidence of the order of the genes except that Vg is between br and f.

5. Tests of knotted, perhaps involving an inversion - Bryan (N.L. 1938, p. 5) reported Kn in this relation: br 7.2 f 27.0 Kn 24.1 Bm2. My last year's report (N.L. 1940, p. 17) was: an 22.5 Kn 25.2 Bm2 and an 22.6 Kn 9.6 gs. These 1940 reports were condensed from five-point tests including also br and f. In the five-point records given here those reported last year are combined with those obtained last summer.

Tests involving Kn

	+	:	br		+	:	br		+	:	br
	+	:	f		+	:	f		+	:	f
Regions	+	:	an		+	:	an		+	:	an
	Kn	:	+		Kn	:	+		Kn	:	+
	+	:	gs		+	:	bm2				
0			82				140				107
1			4				4				
2			3								
3			23				46				44
4			6				39				
1-2			7				2				
1-3			1				1				
1-4							2				
2-3			1								
3-4			1				19				
1-2-3			4				1				
1-2-4			<u>1</u>				<u>2</u>				<u> </u>
Total			133				256				151

	br-f	12.8	br-f	4.7	br-f	0
	br-an	6.8	br-an	2.7	br-an	0
Per cent	br-Kn	26.3	br-Kn	28.1	br-Kn	29.1
Recom-	br-gs	30.8	br-bm2	35.9	f-an	0
bination	f-an	12.0	f-an	2.0	f-Kn	29.1
	f-Kn	27.1	f-Kn	27.3	an-Kn	29.1
	f-gs	30.1	f-bm2	35.1		
	an-Kn	22.5	an-Kn	26.2		
	an-gs	27.1	an-bm2	35.5		
	Kn-gs	6.0	Kn-bm2	24.2		

It is obvious from these records that Kn is between an and gs and relatively near the latter. The recombination percentages for regions to the right of an are about those usually observed, but those in regions between br and an are far from normal. These differences in the two regions to either side of an are seen more readily perhaps when the data are assembled as three-point tests:-

<u>+</u> <u>Kn</u> <u>+</u>	<u>0</u>	<u>1</u>	<u>2</u>	<u>1-2</u>	<u>Total</u>
an + gs	96	29	7	1	133
		21.8%	5.3%	0.8%	
<u>+</u> <u>Kn</u> <u>+</u>	146	47	43	20	256
an + bm2		18.4%	16.8%	7.8%	
<u>+</u> <u>+</u> <u>+</u>	507	12	4	17	540
br f an		2.2%	0.7%	3.1%	

The data of the br-f-an array might indicate that the order of genes is not that given here. But the only order suggested by these data, on the basis of the usual criteria of three-point tests, is br-an-f. Since the chromosome-1 tester stocks employed in these tests are the same ones used in other tests (sections 1 and 2 of this report), no such assumption is tenable. It seems more likely that we are here dealing with a heterozygous inversion involving much of the region from br to an. This assumption is supported by the marked reduction in observed percentage of recombination, particularly in the f-an region, and by the appearance of more double crossovers than of singles in either region.

6. Tests of miscellaneous genes with chromosome-1 markers - Twelve genes, whose linkage had not been previously determined, have been tested with several chromosome-1 markers. Tests of some of these were reported last year (N. L. 1940, p. 18) with only one clear indication of linkage, namely, bm2 with vl9. The data given in the accompanying table were obtained from F₂ cultures of last summer. Percentages of recombination have been calculated with the help of Immer's tables. Many of the relatively large deviations from 50 per cent are not statistically significant. Percentages that show significant deviations from 50, or deviations on the border line of significance, are accompanied by their respective probable errors. The tests of this year are inadequate for much of the short arm of chromosome 1, since, except for sr, the markers used are all in the long arm.

The frequency arrays for bm2 and vl9 from last year's report and from records of last summer are:

	$\frac{+}{vl9} \frac{bm2}{+}$	++	<u>bm2</u> +	+ <u>vl9</u>	<u>bm2</u> <u>vl9</u>	Total
N. L. 1940, p.19		42	25	21	0	88
New cultures		<u>60</u>	<u>42</u>	<u>37</u>	<u>6</u>	<u>145</u>
Total		102	67	58	6	233

Recombination percentage = 16 ± 4.3

It seems clear that vl9 is in chromosome 1. Attempted tests with gs have failed. It is not known, therefore, whether vl9 is to the left or the right of bm2.

Tests of non-linked genes

Chromosome-1 markers

New genes	<u>sr</u>	<u>msl7</u>	<u>br</u>	<u>f</u>	<u>an</u>	<u>gs</u>	<u>bm2</u>
at	58	-	49	54	52	43	42
bm3	50	-	57	48	57	41	-
g2	51	-	40	46	46	36±4.5	34±3.7
ms5	60+	-	38±4.2	47	37	41	53
ms6	55	-	41	41	34±5.9	35	42
ms9	36	-	32±7.1	-	-	-	-
msl0	-	-	47	37±4.9	44	-	52
msl3	53	-	46	49	49	60+	-
msl4	-	-	41±4.2	41±4.2	40±4.3	49	-
na2	48	55	-	-	38	40	-
yg3	46	-	47	47	38	-	38
vl9	42	-	44	55	38	-	23±5.3
*vl9	-	P52	58	-	51	-	<19

* From N. L. 1940, p. 18

R. A. Emerson

1. Some additional data on chromosome VII. Field counts.

(a) $\frac{+ + +}{v5 \text{ ra gl}} \times v5 \text{ ra gl}$

<u>0</u>	<u>1</u>	<u>2</u>	<u>1 & 2</u>	<u>Total</u>
686	52 6.7%	41 5.2%	3 .4%	782

(b) $\frac{+ + +}{ra \text{ gl ij}} \times ra \text{ gl ij}$

<u>0</u>	<u>1</u>	<u>2</u>	<u>1 & 2</u>	<u>Total</u>
169	10 4.6%	35 16.1%	4 1.8%	218

(a) $\frac{v5 \ 7}{ra \ 6} \frac{gl}{gl} \ 18 \ \frac{ij}{ij}$

(c) Antherless (at), unlinked, is very clear cut and gives sharp classifications in the field. An F_2 involving at, v5, and ra showed at to be independent of the other two genes.

(d) In making notes on v5, it is best not to wait until toward the close of the growing season. A number of plants often develop stripes only on the lowest leaves. These should be marked, since if seasonal or soil conditions are adverse, the lower leaves may die and such plants will be classed as green.

A. C. Fraser

(a) Any virescent-1 stock coming from the Co-op or from me must be used cautiously; there seems to be another virescent mixed in. Can anyone send me a stock known to be yl?

(b) In a backcross of about 400 seedlings the alien virescent mentioned above showed no linkage with wx. Of the 182 virescents in this backcross, 108 of them showed normal green stripes. This is suspiciously close to a 9:7 ratio.

(c) A number of chlorophyll types (g, w, l and v) are being inbred by repeated backcrossing to the same inbred. The purpose is to get genetically uniform types for physiological study. Seed of the various types (twice backcrossed) are available to any one desiring it.

(d) In connection with the above mentioned inbreeding program, I should like very much to obtain seeds of two or three different pale greens (esp. lethal ones) and of any other green seedlings that die. Will several of you who have such stocks send in a few seeds, please?

(e) Can anyone send me some g3 seed? That in the Co-op seems not to carry g at all.

(f) A summary table of all my slit blade cultures is given below to show some of the abnormal ratios obtained. The division of the F_2 cultures into groups is arbitrary and hard to justify except on the grounds of convenience. Note that both B.C. & F_2 totals show too many Sb plants.

	<u>Sb</u>	<u>sb</u>	<u>Ratio</u>
Sum of B.C.	495	384	1.29:1
Sum of F ₂ (less than 4:1)	3083	1001	3.08:1
Sum of F ₂ 4:1-7:1	2138	458	4.67:1
Sum of F ₂ (greater than 7:1)	<u>633</u>	<u>69</u>	<u>9.2:1</u>
Sum of all F ₂	5854	1528	3.83:1

(g) Small F₂'s last summer showed no linkage of bm3 or wa to sh, wx, or gl4; nor of sb to lg2, Ts5, j, sh, wx, gl4 or gl. Several attempts have failed to show any linkage of my gl4 to yg, sh, or wx. (This is not the gl4 of Burnham.)

John Shafer

Cornell University and the
United States Department of Agriculture

1. Trisomic stocks. An effort was made during the summer of 1940 to assemble a set of all the known trisomic stocks, to produce stocks of those which were missing, and to make appropriate crosses to build up reserve stocks of all of the trisomes for the future use of cooperators. It was found that seed was available of all of the trisomes except one and four. Individual trisomic plants lacking B chromosomes were selected by actual chromosome counts in each of the eight available stocks. Genetic tester stocks were also examined cytologically in an effort to get together two complete sets of testers lacking B chromosomes, each set to have different endosperm or seedling genes with one good gene in each chromosome. These two sets of testers to be used for crossing alternately with the different trisomic stocks in order to maintain vigorous, genetically identifiable trisomic stocks for general use. Unfortunately, several of the present trisomic stocks are very much lacking in vigor and uniformity and are segregating for various lethals, with the result that although we started the season with five or more trisomic seedlings in each of the eight stocks, at

the end of the season we had not more than one or two poor trisomic ears from two or three of the stocks. But from the other trisomic stocks we have anywhere from 3 to 10 good trisomic ears.

It is especially important in working with trisomic plants to have vigorous, uniform stocks. A number of the trisomic types are inherently weak. In fact the trisomic plants in most of the trisomic stocks apparently come chiefly from the smaller seeds and are apt to be weaker than their disomic sibs in the seedling stage; at least it was our experience that from 75 to 90 percent of the smallest seeds from trisomic ears of the 8 different trisomics we worked with produced trisomic individuals. It would be highly desirable also to maintain a high degree of uniformity of plant type in the trisomic stocks in order to be able to pick as many as possible of the trisomic individuals on the basis of their phenotypic appearance. As an experiment in this direction, we crossed a number of different trisomic plants with pollen of several different inbreds which were known to contain no B chromosomes to see what the trisomics would look like in the various F₁ populations. In our cultures last summer we could, with reasonable accuracy, distinguish the trisomic plants from their disomic sibs in our stocks of numbers 5, 8, and 9, with indications that at least several others could be detected phenotypically in more uniform material.

Another procedure for obtaining very uniform trisomic stocks is to isolate the various trisomes from the selfed progeny of triploids obtained by intercrossing diploids and tetraploids derived from a common inbred parent. In attempting to do this we have learned from experience that it is advisable to start with a very vigorous inbred; otherwise the triploid progenies from which the trisomes must be isolated are rather weak and not too satisfactory to work with.

It is expected that the two missing trisomes, numbers one and four, will be available for distribution next year. Selfed ears showing trisomic ratios for su and similar material segregating for bm2 were obtained last summer from individual plants in triploid progenies known from chromosome counts to have from one to three extra A chromosomes.

Technical assistance for much of the routine cytological work in connection with these trisomic stocks was furnished by the Maize Cooperation.

2. Genetics of the B chromosomes and their derivatives.
The B chromosomes are by no means genetically impotent as was formerly believed and is still being reiterated in current literature on maize cytogenetics. It is true that in small

numbers they appear to produce no discernible effects; they are transmitted more readily than any known A chromosome fragments through both pollen and egg and their presence in genetic stocks seems not to have interfered with genetic analysis of mendelizing characters. But this does not necessarily mean that they are genetically inert or devoid of hereditary potentialities. In summarizing my data on the behavior of the B chromosomes that have been accumulated over a period of years in attempts to solve the enigma of their origin and fundamental nature, there are some rather interesting conclusions that can be drawn with reasonable assurance that they may mean something.

Although individual plants with relatively few B chromosomes are indistinguishable from their no B sibs, higher numbers of B chromosomes produce marked effects: More than 13-15 cause some reduction in fertility; more than 23-25 cause a marked reduction in both fertility and vigor; more than 30 occur rarely and the plants are very weak, produce mostly aborted pollen and set little or no seed.

In reciprocal crosses of plants with 1 B x 0 B, the B chromosome is transmitted about equally well by the pollen and egg to about one-third of the progeny. Exceptional plants with 2 or more Bs appear in these crosses more frequently when the B is carried by the pollen parent.

Reciprocal crosses involving 2, 3, and 4 Bs with no B plants are markedly dissimilar: when the Bs are carried by the seed parent, the numbers in the progeny tend to be intermediate between the parental numbers, but when they are carried by the pollen, the 0 B, 2 B and 4 B classes are predominant. This was true of both meiotic and somatic counts, the total number of individuals involved in these crosses being 398.

The B chromosome plants do not breed true for any given number of B chromosomes, regardless of whether the number is odd or even. When selfed, or when plants with the same number of Bs are sib crossed, less than one-third of the progeny have the parental number of B chromosomes. Various numbers are represented in the populations, the mean number being approximately the same or slightly less than the parental number for plants with from 1 to 17 B chromosomes. The total number of plants studied in these selfed and sib-crossed progenies was 988.

Numbers higher than either parent appeared frequently in crosses between plants with different numbers of Bs ranging from 1 to 20, but in the progenies of plants with more than 20 Bs they appeared less frequently. The mean

number of Bs in the progenies of plants with from 1 to 10 Bs when intercrossed was essentially the same as the mean parental number; with higher parental numbers whose means ranged from 11 to 20.5 the mean number in the progeny was less than the parental mean by from 10 to 30 percent. These data were from 65 cultures which included a total of 983 plants.

Irregular assortment in meiosis, somatic nondisjunction and double division in somatic mitosis possibly due to irregular timing of centromere division, are some of the characteristics of B chromosome behavior responsible for the extreme variation in number observed in the progenies of B chromosome plants. Although the number of Bs in an individual plant is not necessarily the product of the contributing gametic numbers since changes in number may occur in outogamy due to mitotic irregularities there is little evidence of selective elimination of gametes except among very high B chromosome plants. There is no evidence from these experiments on the breeding behavior of the Bs to support the contention of Darlington, presented in a recent discussion of "the activity of the inert chromosomes" (sic) in maize, that there exists a population pressure maintaining an equilibrium distribution of the B chromosomes at relatively low levels in different stocks. In fact the results suggest that higher numbers than are present in most natural populations would readily be tolerated. It seems quite possible that the B chromosomes are on the increase in at least some varieties of maize.

No disturbed ratios were obtained from F_2 and backcross data involving B chromosome stocks crossed with 43 known genes distributed throughout the 10 linkage groups. The linkage relations of these genes are indicated on the accompanying map in which the tested genes are underscored. This map also includes tentative assignments of centromere positions based on information kindly furnished by Anderson, Rhoades and Burnham, the more definitely placed centromeres being represented by an oval drawn with a solid line and those less definitely placed being similarly represented by a dotted line. Disturbed ratios have been obtained with the gene sb, together with some evidence that the reduction in the number of recessives in the segregating progenies was proportional to the frequency of the B chromosomes. (See also Shafer's discussion of sb ratios in this News Letter) This would be expected if the B chromosomes carried the normal Sb allele. Unfortunately the linkage relations of sb are unknown.

These gene tests involving the B chromosomes have an important bearing on the fundamental question of the origin of the B chromosomes. If the centromere positions indicated on the linkage maps are even approximately correct, it is

apparent that the tested genes giving undisturbed ratios in the presence of B chromosomes are distributed among 17 of the 20 normal A chromosome arms. Only 3 arms, the short arm of 8 and 10 and the long arm of 9, do not include at least one tested gene. If a test of one or a few genes were sufficient to exclude a particular chromosome arm from further consideration as the source of the B chromosome, the problem of the origin of the Bs would be much simplified, but in my opinion such tests would not be sufficient. It is altogether possible, in my opinion, that only part of a particular arm is represented in the B chromosome. For example, it might consist of an A chromosome centromere plus some adjacent euchromatin, but not necessarily all of the euchromatin of any particular arm, and in addition heterochromatin from the same or some other chromosome. This suggestion as to the possible mode of origin of the typical B chromosome may seem unnecessarily involved. However, there is a rapidly accumulating body of evidence that the chromosome is not as stable a unit as it was once thought to be. In fact it is surprising that chromosomes maintain any individuality whatever as separate and distinct morphological entities for extended periods of time in the light of the numerous types of reorganization to which they are subject. Furthermore, the typical B chromosome has a distinctive prophase morphology unlike that of any one region of similar length among the A chromosomes ordinarily present in existing types of maize. This is not an off-hand statement based on casual observation, but is the conclusion arrived at after making a very critical survey of the meiotic prophase morphology in well over fifty varieties of maize representing all of the known types of flour, flint, dent, pop and sweet corn, a survey that was conducted primarily to throw light on the origin of the B chromosomes. This does not mean that there may not be in existence today types of maize containing an A chromosome or segment thereof that is identical with the B chromosome. Or it may be that such a chromosome existed in primitive strains of maize that are no longer in existence. The fact that the B chromosome ordinarily does not synapse with any of the A chromosomes suggests that it is not of recent origin, but synaptic behavior alone should not be considered as proof of this assumption.

There is the further possibility that hybridization with relatives of maize may have been involved in the origin of the Bs, but in my opinion the possibilities of a more direct mode of origin are by no means exhausted.

In a further search for clues to the origin of the Bs, it would seem highly desirable to examine additional types of maize especially from regions where primitive stocks may still be in existence. Also more extensive tests of known genes should be made in the search for alleles of B

chromosome genes; possibly Sb is one such allele, but additional cytological and genetical tests are needed to establish this. If the suggestion made above concerning the origin of the Bs is valid, and if there is a tendency in maize as in *Drosophila* for heterochromatic regions to be populated with fewer genes than are the euchromatic regions, the best chance of finding alleles of known genes in the B chromosome would be to test especially genes lying near the centromeres in the linkage maps. These genes may actually be an appreciable distance cytologically from the centromeres. But if the proximal euchromatic region of the B is in approximately the same relative position with reference to the centromere that it was in the A chromosome from which it originated, some of these nearby genes should be represented by alleles in the euchromatin of the B, which constitutes approximately one-third of the total length of the chromosome. A certain number of these nearby genes have already been tested as indicated on the linkage map. An especially good test involved chromosome 5 in which Rhoades' data from his telocentric fragment has given us the best evidence we have of the location of a particular centromere relative to neighboring genes. His evidence tells us that the closely linked genes, bm and bt, are definitely on opposite sides of the centromere. These two genes, as well as a2 in the short arm and bm, pr and y2 in the long arm of this chromosome gave normal backcross and F_2 ratios in the presence of B chromosomes. Thus these tests would seem to exclude the possibility that the regions in which they are located are involved in the makeup of the B chromosome.

A notable characteristic of the B chromosomes is that they are like the A chromosomes in being susceptible to breakage, with the resultant loss of acentric segments of chromatin or rearrangement of parts. But there is this distinction that the supernumerary B chromosomes can undergo a greater variety of such morphological changes than can the A chromosomes without deleterious effects, and their monocentric derivatives can be readily maintained in culture for further study. Over a period of years a considerable number of such B chromosome derivatives have arisen in my stocks, the first of these being the C chromosome that was described back in 1928. Since most of these elements have been detected in root tip figures being examined for chromosome count, they have been grouped for convenience in four reasonably distinct size classes or types, based on their appearance in the somatic metaphase. These include (a), the C type that is somewhat shorter than the B chromosome but definitely elongated in contrast to (b), the D type that is essentially spherical with a diameter roughly equivalent to the diameter of an ordinary chromosome, (c), the E type that is of approximately the same size as the undivided satellite of chromosome 6, and (d), the F type that is distinctly smaller than the E type and in fact is

only slightly above the lower limit of visibility of the photomicroscope.

On the basis of this classification there can be no additional new types of still smaller B chromosome derivatives, at least not until the electron microscope is utilized in the study of chromosomes. (Incidentally, this series of chromosome types from B to F, if interpreted in the reverse order, makes a very convincing demonstration of the de novo origin of chromosomes.) In the meiotic prophase morphological distinctions within these size groups can be detected and may be classified accordingly.

The B chromosome derivatives are proving very useful in studies of the relative genetic potency of different parts of the B chromosome. Data are available at the present time which suggest that the sterility-inducing effects of the B chromosome are to be attributed to factors localized chiefly in the proximal euchromatic region of the chromosome.

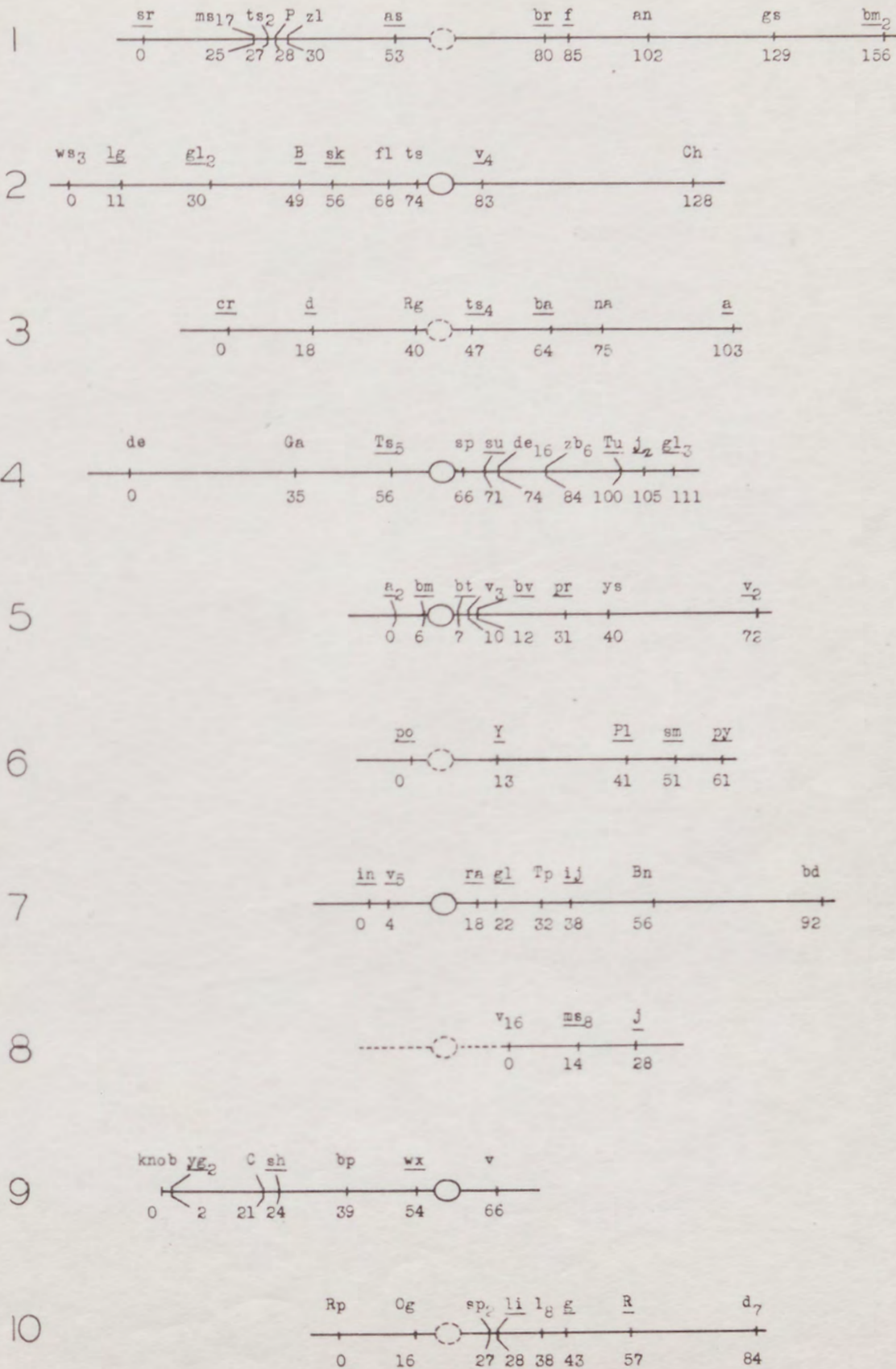
There is some evidence that other mutant derivatives of the typical B chromosome, such as extensions of the long arm or additions to the rudimentary short arm, occur from time to time, but these are less easily detected in somatic figures because of their greater similarity to the shorter A chromosomes.

The occurrence of distinctly dibranchial B type chromosomes in maize has been described from somatic figures by Darlington and others in recent years. But in these cases the position of the centromere has very probably been misinterpreted. The typical B chromosome when viewed in somatic metaphases often exhibits what appears to be a subterminal constriction, especially after fixation with fluids that shrink the chromosomes. This is not a true centric constriction but is actually the weakly chromatic region between the proximal knob adjoining the centromere and the distal heterochromatic portion of the chromosome. This interpretation is quite obvious if one is familiar with the pachytene structure of the B chromosome and follows the transformation accompanying the shortening of the B chromosome during the late prophase and early metaphase of the first microspore division where the distinction between euchromatin and heterochromatin in these stages is clearly apparent in good preparations. Many pachytene figures of the typical B chromosome do, however, show the presence of a rudimentary short arm consisting of a very few small chromosomes. This arm is often folded back against the proximal knob on the opposite side of the centromere, thus making the centromere appear truly terminal.

L. F. Randolph

MAIZE LINKAGE MAPS

WITH TENTATIVE ASSIGNMENTS OF CENTROMERE POSITIONS



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1. In further studies on genes h (starchy endosperm) and fl2 (floury endosperm), h was found to be hypostatic to su1 and wx; and fl2 hypostatic to su1. Gene h is linked with fl2 with 4% crossing-over, and with dl, with 25% crossing-over. This puts both genes in chromosome 3, but the exact loci are not yet determined. If it is assumed that h is approximately at 60, then fl2 would be near ts4 or Rg.

W. J. Mumm

1. A sugary type of endosperm which was discovered at this Station several years ago appears to be identical with su2 as indicated by crosses. In inbred Os 426, one of our hybrid corn producers, Robert Bear, Decatur, Illinois, found an ear segregating for yellow vs. white endosperm, and normal vs. viviparous kernels. All the normal kernels were yellow and all the white viviparous. The gene for vivipary involved is likely vp5 which Doctor Lebedeff reported in the 1940 News Letter. Another of our hybrid corn producers, Royal Oakes, Bluffs, Illinois, discovered a dwarf in a double cross. This dwarf as grown in 1940 was 56 cm. high; tassel, large, spreading, and productive of pollen; and leaves large and dark green giving a vigorous appearance to the plant. Crosses indicate the gene involved is not dl, and the new dwarf does not answer the description of other dwarfs listed in Cornell Memoir 180.

C. M. Woodworth

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1. A valuable mutation. The ministry of agriculture in Venezuela has received numerous requests from the farmers for a variety of sweet corn which would do well under tropical conditions. There has been no way of filling these requests, however, because Venezuela has no sweet corn of its own, and all the imported varieties have failed to give desirable results.

There are at least two ways of getting good sweet corn for this country. One is to import unadapted varieties of sugar corn and cross them with the adapted varieties of starchy corn and continue selfing and back-crossing until the sugary character becomes established in an adapted variety. Another method is to make a large number of selfs in the best varieties of starchy corn and watch for the appearance of sugary as a result of a mutation. This is the procedure that was chosen, mainly because inbred lines were needed anyway for the production of hybrids. In September, 1939, 135 varieties of open-pollinated corn from various countries were planted to select the best ones and to make selfs.

During the first two generations of inbreeding, there were no mutations to sugary in approximately 3,000 selfs. In the third generation, however, in which there were approximately 1,500 selfs, two ears segregated for sugary. One of these was in the best inbred line that had been developed from an open-pollinated variety from Cuba and is probably sugary-1 (su). It segregated 216 Su to 72 su. The other sugary appeared in another inbred line from the same source and may be su^{am}. This ear had 478 kernels of which 10 were very sugary, 106 had a dull endosperm, and in the remaining 362 kernels there was a continuous gradation from slightly dull to clear endosperm. Test for allelism with known stocks of su and su^{am} will be made.

Some of the seeds from these two ears have been planted and there should be no question about the development of suitable sweet corn varieties in the near future.

2. Late plants. Two second generation inbred lines segregated for late-maturing plants in 1940, but there were numerous differences between the late segregates of one culture and those of the second culture. Inbred line number 40-156 consisted of 10 plants of which 8 grew normally and produced ears, one grew about 7 months without shedding pollen, and one which was apparently a late type was broken by a workman. Inbred line number 40-290 consisted of 5 plants of which 3 were like the normal plants of 40-156 and two were late like those of the other culture but differed from them in that they were dwarfs instead of giants.

Culture	Type	Days of Pollen to Plant	Total number of nodes	Nodes with brace roots above ground	Height cm.	Length of first 5 inter-nodes cm.	Average circumference of first 5 internodes cm.
40-156	:Late	:207++	: 26	: 15	: 255	: 11.0	: 10.8
40-156	:Normal	:104	: 14	: 1	: 184	: 12.6	: 7.3
40-290	:Normal	: 98	: 13	: 1	: 175	: 12.0	: 7.1
40-290	:Late	:207++	: 21	: 11	: 33	: 1.2	: 6.0

The late types died about January 15, 1941 from lack of water. The giant plant from culture 40-156 subdivided near its top, producing 10 branches each of which contained a small tassel that was nearly exposed at the time the plant died. This giant type may be the same mutant character that was originally reported by Brunson and has since appeared in the cultures of Bryan and Emerson.

The dwarf type of late plant in culture 40-290 still had its tassel deeply enclosed in the leaves when it died from lack of water. Perhaps this mutant form of plant is the same as the one described by Antonio E. Marino in "Una variacion 'tardia' en maiz" (A late variation in maize), Revista Argentina Agron. 6 (3): 237-240, 1939.

3. In three different inbred lines of corn, ears have been found in which there is no definite orientation of the kernels in spite of the straightness of the rows. The germ of the kernel may face the tip, or the butt, or either side. Other ears in the same cultures were normal.
4. Twin kernels. One ear in a second generation inbred had 287 kernels of which 68 were normal; 210 had streaks on the backs of the kernels, indicating a tendency toward the production of another germ; and 9 had two fully developed germs, one on each side of the kernel. Apparently the tendency toward twinning segregates about 3 to 1.
5. Hard starch vs. soft starch. Among 140 self-pollinated ears in second generation inbred lines developed from an open-pollinated variety of flint corn, one ear was found in which 130 kernels were of the flint type and 41 were capped with soft starch. The segregation was discontinuous. There were no "dents" in any of the kernels.

D. G. Langham

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Linkage Tests

Chromosome 10.

<u>Genes</u>	<u>Phase</u>	<u>XY</u>	<u>Xy</u>	<u>xY</u>	<u>xy</u>	<u>Total</u>	<u>% Recom.</u>
<u>Og na2</u>	CB.	39	20	37	50	146	39
<u>Og na2</u>	CS	129	40	39	21	229	42

Note on na2 = Material from Cornell under No. Co 37-172 and designated na2.

<u>gl d7</u>	CS	53	9	17	4	83	45
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Mutation - YY → Yy. Verification of this one-kernel mutant from over 7200 kernels reported in 1940 News Letter. This white was tested against the y gene in Evergreen sweet corn, in a white dent inbred and in Hickory King. All progeny were white, indicating that this mutant involved the standard Y gene.

E. W. Lindstrom

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"Intersectional" hybrids (Corn Belt lines crossed with local strains) of the following types have been tested: single crosses, top crosses, multiple top crosses, three-way crosses, and double crosses. The average of all "intersectional" hybrids was 20.8 percent in 1939 and 18.2 percent in 1940, higher than the average grain yield of the local varieties. These hybrids were made up entirely at random except for morphological observations of the parent lines. Besides grain yield the "intersectional" hybrids approach or equal the local varieties in pest resistance and grain quality. When compared with Corn Belt double crosses, the "intersectional" hybrids are much superior in general adaption to North Carolina conditions.

In six locations across the state 5 x 5 lattice square designs on 1/140 acre plots were utilized in 1940. The lattice square design showed an average gain in precision of at least the equivalent of an extra replication in a complete randomized block design. Complete randomized blocks of more than 30 entries have proved very unsatisfactory in our studies. Since 5 x 5 lattice squares have been of doubtful value in the Corn Belt, it seems worthwhile to mention our results on the heterogeneous soils of the Southeast.

Paul H. Harvey

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1. A new gene for pollen abortion, pa, is located in chromosome 1. Plants heterozygous for pa are semisterile in the pollen and have normal ears. It is transmitted rarely if at all through the pollen, but gives normal ratios through the eggs. The locus of pa is between P and br, the recombination values being: P-30-pa 34 br. It differs from sp and sp2 in that pollen carrying it is for the most part devoid of starch.

Cytological examination shows no visible deficiency in chromosome 1.

C. R. Burnham

The following chromosome map shows the loci of those interchanges for which there is cytological information. It is based on data presented in previous Coop Letters, whatever has been published and in addition unpublished data of Dr. C. R. Burnham. The scheme Anderson has used is followed, the breakage points being measured from the spindle fiber insertion region in tenths of the length of the particular arm in which the break occurred. Interchanges for which only genetic information is available are not listed.

As is customary, the map presents the cytological lengths of the chromosome which are in proportion, using chromosome 10 as 100 units. The length of each arm is given at the spindle fiber attachment region, the total chromosome length being the total of the two arm lengths. The long arm/short arm ratio is given at the bottom of the map.

The following example illustrates the use of the map: translocation 1-2a is listed as 2a on chromosome 1 opposite .7 on the long arm; on chromosome 2 it is listed as 1a opposite the locus .6 on the long arm. When more than one break has occurred at the same point, they are grouped together. For example, there are 5 translocations at locus .3 on the long arm of chromosome 2. Breaks which have occurred in the satellite of chromosome 6 are grouped in that region but their position in the satellite arm is not definitely known. 6-9a occurred in the nucleolus-organizer region. 2-6a and 5-9a involved the short arm of chromosome 6, but their relation to the spindle fiber insertion region is not known, hence they are given 0+ ratings.

On completing this map Dr. C. R. Burnham has given advice and suggestions and a final check on the figures.

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Edward Garber

[illegible]

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Comparison of the Genetic Effects of Xrays and Ultraviolet Treatment. In 1939 and 1940 an attempt was made to determine the relative frequency of mutation and other types of genetic alteration induced by comparable doses of Xrays and ultraviolet. Since there is no physical basis for equating doses of the two radiations, it is necessary to make the comparison on the basis of some biological equivalent, for example, to determine the effect upon mutation of two doses equal in inducing deficiencies or translocations. But since previous studies had shown that the deficiencies and translocations induced by ultraviolet are of types different from those produced by Xrays (or include various types in widely different proportions), the doses equivalent on the basis of one chromosomal effect would be widely different from those equivalent on another.

The doses used therefore were chosen arbitrarily at levels suited to the significant determination of mutation frequency, and their equivalence may be judged only by the frequencies of the various alterations detected. The Xray doses used are relatively low, so as to permit the survival of as many plants as possible and the production of well-filled ears, which is essential for the determination of mutation rates. The ultraviolet doses used are close to the tolerance limit for the wave lengths represented.

Since both types of radiation produce defective plants of various kinds, it is essential to reduce losses to a minimum and to consider the individuals lost as well as the survivors in the interpretation of the results. The populations used represent the entire seed population from the treated ears, and special precautions were taken to secure maximum germination and survival. Plants which died early or which failed for other reasons to yield a pollen specimen were classified as "+" (apparently normal plants, accidentally lost) and "-" (apparently defective plants). The treatments compared, populations used, frequency of endosperm deficiency (A, Pr, Su), and losses to pollen shedding are shown below:

	No. Seeds	Endo-: sperm: deficien-: %	Embryo-: tion	Un-germi-: nated	Lost Died Early +	-	No Pollen +	-	: Excluded	: Hap-: loid	: Contam-: inated	: Popu-: lation		
λ3022	210	43.1	:	19	12	10	8	0	0	:	2	0	:	159
λ2967	160	28.8	:	7	10	1	3	0	2	:	1	0	:	136
250 r	420	3.0	:	11	11	3	7	1	1	:	0	2	:	384
500 r	217	7.4	:	8	7	3	4	2	4	:	1	0	:	188
Control	1016	0.3	:	8	9	20	1	0	1	:	2	0	:	975

Frequency of Pollen Segregation in F_1 . In populations so large as those required for the determination of mutation rates (particularly with low doses and control progenies), it is not feasible to determine the frequency of deficiencies and translocations by the direct cytological examination of every plant. Some indications regarding the frequency of chromosomal derangements may be obtained from the frequency and type of pollen segregation in F_1 . Pollen segregation was recorded as to percentage and type of defective pollen, the types ranging from "a" (significant reduction in size but normal development of contents) to "e" (practically empty). In the table which follows, types a and b are listed as "subnormal", types c, d, and e as "aborted," and segregations of both classes in the same individual as "mixed,"

The following facts determined from investigations in previous seasons are of help in the interpretation of the pollen records:

(1) "Directed segregation" in maize translocations is absent or extremely rare. The plants with segregating defective pollen therefore include all of those in which translocation has occurred as well as those with deficiencies.

(2) Gametophytic lethals at points of translocation are absent or very rare. If, as a result of "position-effect" or other causes, there were a tendency for mutational effects at the breakage points, it might be expressed by failure in development or functioning of the pollen carrying the translocation chromosomes. This does not occur. It is therefore possible to discriminate between segregating defective pollen due to translocation and that due to deficiency by transmission tests.

(3) F_1 plants with segregating defective pollen include many with cytologically detectable deficiencies not associated with translocation. Among pollen segregating plants from Xray treatment, these deficiencies include some which are obviously intercalary. Most of the cytologically detectable deficiencies are found in plants with "aborted" pollen, but in short intercalary deficiencies defective pollen is frequently of the "subnormal" class. The deficiencies from UV observed cytologically include none which is clearly intercalary. In all of the UV deficiencies so far observed cytologically the segregating pollen is of the "aborted" type.

(4) Among the plants with segregating defective pollen, the proportion due to translocation is much lower with ultraviolet than with Xrays. With high doses of ultraviolet, translocations unquestionably are induced, but the great majority of these are "deficiency-translocations"; that is, plants in which one or both of the chromosomes involved in the translocation has lost a segment. These deficiency-translocations are usually very defective plants, and their frequency depends in large part upon the precautions taken to insure survival of the poorest plants of the progeny. Translocations of this type may not be detected by transmission tests; they may be identified only by direct cytological examination of the F_1 .

The frequency of segregating defective pollen in these cultures is listed in the next table. The numbers and percentages given in parentheses represent the frequencies when each "high-sterile" is taken to represent two segregating factors for sterility.

	No. Exam.	Semi-sterile			High-sterile			Low Sterile	Total	%
		Sub.	Ab.	Mix.	Sub.	Ab.	Mix.			
A3022	159	10	15	1	0	2	3	1	32(37)	20.1(23.3)
A2967	136	13	8	0	1	2	1	2	27(31)	19.9(22.8)
250 r	384	13	23	2	0	8	2	1	49(59)	12.8(15.4)
500 r	188	9	21	6	0	12	6	5	59(77)	31.4(41.0)
Control	975	3	4	0	0	0	0	2	9(9)	0.9(0.9)

Low Deficiency Rate in Embryo vs. Endosperm with UV. In both UV progenies the frequency of plants with segregating defective pollen was about 20 per cent. There is reason to believe that many of these are due to causes other than deficiency (notably to mutations producing subnormal pollen). But even if all were due to deficiency, their frequency is

far lower than would be anticipated from the endosperm deficiency rates. The seeds planted showed endosperm deficiencies amounting to about 36 per cent for the marker genes A, Pr, and Su; these could represent only a small fraction of the deficiencies present in the entire ten chromosomes of the treated gamete. With equal deficiency frequency in the embryo, almost all of the F₁ plants should have segregating defective pollen due to deficiency, and many should have several deficiencies.

At one marked locus, a direct comparison may be made. The seeds planted in the two UV progenies included 71 endosperm deficiencies for A; the F₁ plants included no A-deficiencies.

Although induced deficiencies are relatively rare in the F₁ embryos, it is certain that they are not wholly absent. The treated pollen carried the dominant markers A B Pl R^r; the UV families included five genetically marked deficiencies and several unmarked deficiencies which were identified cytologically in defective plants. Only one deficiency (a monosomic for chromosome #6) was found in the much larger control population.

Frequency of Translocation. In certain cultures, translocation frequency was determined by direct cytological examination of the F₁ plants in every plant with segregating defective pollen. The cultures examined included the entire population given the ultraviolet treatment "X2967" and the entire population from one ear given the Xray dose "250 r" and one ear given "500 r." The results are shown below:

Population		Segregating Pollen			Diakinesis Association	
		Semi-Sterile	High-Sterile	Low-Sterile	Inter-change	Deficiency-Association
X2967	136	21	4	2	0	3
250 r	97	14	0	0	4	2
500 r	83	20	7	3	11	6

It is noteworthy that deficiency-associations are found with Xray as well as UV treatment, but in the former they occur with a larger number of interchange-associations, while with the latter they do not.

Frequency of Translocation in Control. The spontaneous frequency of translocation is of interest in determining whether the occurrence of chromosome interchanges following

ultraviolet treatment is an effect of the treatment. Among the translocations observed in UV-treated progenies to date, although as previously mentioned the majority are deficiency-translocations, there are two or possibly three which appear to be regular segmental interchanges. Although such translocations have previously been found in untreated maize populations, there is no basis for an estimate of their spontaneous frequency. The large control in this experiment included only nine plants with segregating defective pollen; the progeny tests from these showed that two of them transmitted through pollen the factor for aborted pollen segregation. Diakinesis examination in these progenies showed in both cases the presence of chromosome interchange producing a ring-of-four at diakinesis. The spontaneous frequency of chromosome interchange thus appears to be appreciable, and the number of interchanges observed following ultraviolet treatment is not significantly higher than that in untreated material.

The results suggest that UV treatments produce a significant increase in the frequency of deficiency-translocations, without appreciable effect upon the frequency of segmental interchanges.

Mutation. The mutations determined were those involving endosperm characters, defective seeds, germless, and seedling abnormalities. Each of these types may be determined by examination of the selfed ears of the F_2 plants or of the 100-seedling progenies grown from each of these ears. All of the mutations which are not clear-cut and unmistakable in the F_2 culture are checked for recovery in F_3 from heterozygous F_2 plants. The analysis of the check-progenies of 1940 is not yet completed, and the data therefore are given separately for number of mutations and number of doubtful mutations, the latter being those subject to the F_3 check. The percentages in the table are provisional percentages representing the clear-cut mutations plus half the doubtful mutations. Confirmation tests so far completed indicate that the final percentages will be somewhat higher than those here given.

	Endosperm				Germless				Seedling				Total %
	n	M	M?	%	n	M	M?	%	n	M	M?	%	
X3022	62	5	5	12.1	110	2	11	6.8	107	11	2	11.2	30.1
X2967	93	4	8	8.6	82	0	6	3.7	81	4	1	5.6	17.9
250 r	250	1	2	0.8	298	0	1	0.2	299	1	2	0.7	1.7
500 r	143	5	7	5.2	133	1	2	1.5	126	1	1	1.2	7.9
Control	613	0	7	0.6	766	0	1	0.1	764	1	2	0.3	1.0

The mutations included, together with many useless types, a scattering of promising viable mutants affecting endosperm and seedling characters. The number of mutants is considerably larger than that shown in the table, since several other treatments were handled similarly. In all of these the F_2 ears which yield the mutations are segregating for \underline{Y} and \underline{P}_1 , permitting a three-point test for chromosome 6 mutants, and are segregating also for single markers on chromosome 2, 3, 4, 5, 9, and 10. Doctor C. R. Burnham is undertaking the location of some of the more promising mutants.

Comparative Mutation Rate from Xray and UV. As the table indicates, mutations were considerably more frequent from UV than from Xrays, in spite of the fact that the Xray doses used produced considerably more translocations and probably more deficiencies.

Actually the mutation rate from UV is considerably higher than is indicated by these data. Among a sample of pollen grains treated with UV, because of the high absorption in passing through the pollen grain contents, only a small proportion receive a heavy dose at the site of the gametic nucleus, and many receive no effective dose at all. The mutation rate among the effectively-treated pollen grains therefore is much higher. Many of these include two or more independent mutations.

It is probable also that many of the segregating pollen defects (particularly of the subnormal class) are due to mutation expressed in the gametophyte generation rather than to deficiency. Since intercalary deficiencies are so rare and mutations are so common with UV treatment, it seems probable that the high frequency of subnormal pollen segregation following UV treatment is largely or wholly the result of gametophytic mutations, and is another expression of the high frequency of mutation induced by this agent.

Technic for Identification of Gametophytic Mutations.

In the mutation technic used in the experiment just described, gametophytic mutations are not detected if they have no visible effect upon pollen development; and if they produce defective pollen, they are not distinguishable from short deficiencies. Another difficulty is that many of the sporophytic mutations are questionable because of possible over-lapping of the normal phenotype.

Both of these difficulties may be avoidable, for limited chromosome regions, by the use of inversions to inhibit crossing-over. A trial of this method with one inversion was made in 1940, in an experiment comparing UV and Xray treatments in a manner otherwise similar to that of the experiment just described. The method may be used more effectively with a combination of inversions in various chromosomes.

The treated parent was I wx; the untreated parent carried rearrangement-9 (McClintock 1939) with i Wx. This rearrangement eliminates crossovers in a large part of chromosome 9. The F₂ seeds therefore are of three types -- one fourth I wx, homozygous for the treated normal chromosome; one fourth i Wx, homozygous for the untreated chromosome; and one half I Wx, heterozygous for the treated and untreated chromosomes. Induced chromosome 9 alterations are linked with I wx. They are manifested in three ways:

(1) By pollen defects linked with wx. In iodine-stained pollen specimens extremely slight effects on pollen size or development may be recognized, far below the limit of detection in unlinked segregation.

(2) By modified ratios for I and Wx. Gametophyte mutations or deficiencies without visible effect on pollen development, if they prevent functioning of pollen, modify the 3:1 ratios to 2:2 and 4:0 respectively. If they permit reduced functioning, they permit the segregation of a reduced proportion of wx seeds. (A reduced proportion of wx seeds may result also from a Ga-mutation inhibiting functioning if separated from the rearrangement by crossing-over.)

(3) By seed and seedling mutations linked with I Wx. Here also the linkage permits the detection of some mutants which would be doubtful or undetectable without linkage.

The mutants are crossed with C Wx (normal chromosome) for genetic location in three-point tests. Gametophyte mutations not transmitted through pollen may be recovered from the heterozygous I Wx seeds, and when pollinated by C Wx (normal) yield heterozygotes in which the location of the Ga-factor may be determined by crossing on C wx or c wx. Deficiencies and other chromosomal alterations not lethal to the female gametophyte may be recovered similarly, for cytological examination in plants free from the rearrangement.

The spontaneous frequency of the various types of alteration is shown in the same F₂ ears by segregations of the same kinds linked with i Wx instead of I wx.

The results of this experiment, as regards chromosomes other than #9, were similar to those of the previous experiment, except for differences incidental to the use of different wave lengths and dosages, which will not be discussed here.

The number of chromosome 9 alterations of each type identified is shown below:

	Treated Chromosome-9			Untreated Chromosome-9
	UV λ2967	UV λ2537	Xray 600 r	
Population	457	263	288	1008
(1) Defective Pollen				
Aborted	2	0	3	0
Subnormal	$\frac{0}{2}$	$\frac{0}{0}$	$\frac{2}{5}$	$\frac{0}{0}$
Total	2	0	5	0
(2) Low Transmission 12 (Pollen Normal)		4	2	0
(3) Mutation				
Endosperm	3	2	0	0
Germless	1	0	0	0
Seedling	$\frac{2}{6}$	$\frac{2}{5}$	$\frac{1}{1}$	$\frac{1}{1}$
Total	6	5	1	1

These constitute a representative sample of the genetic alterations induced by Xrays and UV, all located within a region well suited for critical comparison genetically and cytologically.

Qualitative Comparison of Induced Mutations. The very high frequency of UV mutations, with the much lowered frequency of chromosomal derangements, suggests that these may include types of mutation not included among the Xray mutants, and may be relatively free from the various sorts of pseudo-mutation which occur under Xray treatment as by-products of induced chromosomal derangement.

The problem is to find criteria which may be applied to distinguish types of "mutation." Possible criteria available in maize include the following:

(1) Gametophyte viability. Many induced mutations are of lowered viability in the gametophyte, particularly as shown by reduced transmission through male germ cells. Differences in viability among mutants are usually regarded as characteristic of the different mutant alleles, the higher viability of standard alleles being considered the result of natural selection.

This view is contradicted by results with the known spontaneous mutations in maize. A large number of mutants representing various endosperm genes is available, and in

these gametophyte viability and male transmission are regularly normal. This suggests that the low viability of induced mutants may be due to the loss of something more than the dominant allele which is assumed to have mutated.

Transmission of the mutant through pollen, in competition with the normal non-mutant pollen grains, provides a very rigorous test of gametophyte viability, which may be applied to mutations at any locus.

(2) Use of genes which mutate normally to an intermediate allele. Spontaneous mutations of \underline{R}^r , identified by colorless seeds, are regularly mutations to small \underline{r}^r , as previously reported. Recent studies have shown that \underline{R}^r mutates also, and with comparable high frequency, to \underline{R}^g . It does not mutate spontaneously, or at most does so very rarely, to \underline{r}^g . This may mean that the effect of \underline{R}^r on anthocyanin coloration of the aleurone and of the plant is due to two separate but very closely linked genes, but whether this is true or not, the fact provides a convenient method for distinguishing between spontaneous mutations at this locus and the type of pseudo-mutation which could result from haplo-viable deficiencies.

A similar situation may apply at certain other loci. Recent trials show that the gene \underline{A}^b also mutates spontaneously, with a fairly high frequency, to an intermediate allele. The results of an experiment in which the suspected mutations were identified by loss of aleurone color and all were subsequently checked by progeny tests show the following frequencies:

Stock	Mutation to \underline{a}^p	Mutation to \underline{a}
$\underline{A}^b \underline{A}^b$	0/55,765	25/36,661
$\underline{A} \underline{A}$	0/19,587	0/9,431

The \underline{a}^p mutants, when combined with the appropriate complementary genes, have the red-brown plant color and brown pericarp characteristic of the standard \underline{a}^p , although some of the mutants show a somewhat deeper color in aleurone and plant than the standard. Nine of these mutants have been tested for dominance of the brown pericarp effect. In all of these the effect is dominant as in the standard \underline{a}^p .

(3) Reverse mutability. The analysis of the action of \underline{Dt} by Rhoades makes possible the effective application of this criterion in the case of apparent mutations to \underline{a} .

It is not applicable to the a^p mutations from A^b , since Dt is without effect on a^p . Whether it is applicable to all mutant a 's, or to the colorless mutations from all A 's, also remains to be seen, since the present stocks of a , on which Dt is effective, trace to not more than two original sources. Reversability of a mutant a under the influence of Dt is good evidence against deficiency, but failure of a mutant to be reverted by Dt is not convincing evidence against intragenic mutation.

(4) Detailed analysis of phenotypic effect. In the case of the genes affecting anthocyanin pigmentation, mutant phenotypes may be compared quite precisely by the use of methods developed by Karrer, Robinson, Scott-Moncrieff, and others for the identification of the various anthocyanin pigments. A study of the anthocyanin pigments in maize now being made by J. E. McClary indicates that there is a very rich variety of these pigments in maize, including several which do not commonly occur among the flower pigments genetically studied by the English workers.

One of these is the anthocyanin pigment which occurs together with a flavonol in the a^p stock. In the presence of B and Pl , A^b , like A , produces chrysanthemin, but a^p produces an anthocyanin of distinctly different properties. The dark a^p obtained by mutation from A^b apparently produces the same pigment in larger quantity.

Comparison of Xray and UV Induced Mutations of A.
Mutations and deficiencies involving the A locus may be identified by seedling examination of F_1 plants from the cross $a \times A \ B \ Pl \ R^f$. A very large number of plants of this constitution have been examined following treatment of the male parent with Xrays, and the green seedlings saved for identification of the mutation or deficiency. The majority of such plants turn out to be distinctly defective in growth and to have segregating aborted pollen. A small proportion approximate normal growth, but these also have defective pollen. Among them a few are found with segregating pollen of the subnormal type. Two plants were found in which the A effect had been lost, the plant was of normal vigor, and the pollen was completely normal in appearance. Both plants had the phenotypic appearance of typical $a \ B \ Pl$. They are designated a^{x4} and a^{x6} . In addition one plant of $a \ B \ Pl$ phenotype and normal vigor, but with segregating subnormal pollen, was included in the further tests. It is designated a^{x1} .

In similar progenies of plants from UV treated pollen, the frequency of loss of the A effect is very much lower, as noted in connection with the experiment first described. Such plants may be found, however, by growing large enough progenies of F_1 seedlings, and we have so far identified about fifty of them. Among these, four individuals showed loss of the A effect but fully normal pollen. All of the others had aborted pollen, and in all cases this was empty or nearly empty. Three of the four mutants showed the phenotype of a B Pl. They are designated a^{U3}, a^{U15}, and a^{U18}. The fourth mutant, though green as a seedling, showed faint anthocyanin coloration in later growth and deepened to a light purple at maturity. It is designated A^{lt}.

The chief characteristics of these induced mutants, with reference to the criteria which have been mentioned, are as follows:

(1) Phenotype. Except in the case of A^{lt} no consistent difference has been found in the phenotype of the mutants and that of a. In all six the aleurone is wholly colorless with C R A2, and the plant is typically brown with B Pl. The pericarp is red with A P but has not yet been seen with a P. With a^{U3} B Pl a considerable amount of purple pigmentation was observed, chiefly in the upper half of the lower leaf sheaths, but similar coloration has been found in a B Pl plants extracted from the same culture. In segregating progenies from a^{mutant}/a x a B Pl and a^{mutant}/a x a^P B Pl, it was not found possible to distinguish the mutant a from the standard a in any of these six cases.

The phenotype of A^{lt} is clearly distinguishable from A, a, and a^P in plant color, but it is not always distinguishable from a^P in aleurone color. The plant color at maturity (with B Pl) is more similar to A than to a^P, and the plant does not appear brown at any stage. The cob is reddish purple. The extracted pigment includes a considerable quantity of anthoxanthin as well as anthocyanin. The purified anthocyanin is distinct from both chysanthemin (A) and the anthocyanin of a^P.

(2) Gametophyte viability. a^{X1} is transmitted through female germ cells but in reduced proportion, seldom in more than 30 per cent of the expected number. Seeds heterozygous for the variant are reduced in size. There is no transmission of the type through pollen of the heterozygous plant.

a^{X4} and a^{X6} show full viability in the female gametophyte, and the seeds are full size. Although the pollen in both these types is fully normal in appearance, transmission of

the mutant is reduced in pollinations from heterozygous plants, ordinarily to 25 to 40 per cent of the expected numbers.

Self-fertilization of $\underline{A}/\underline{a}^{X6}$ plants yields no colorless seeds, even though the same pollen used on $\underline{a} \underline{C} \underline{R}$ testers both before and after selfing shows transmission of the mutant \underline{a}^{X6} . This type therefore appears to be zygotically lethal when homozygous. The same result is obtained with \underline{a}^{X4} , though the trials in this case are less extensive.

\underline{a}^{U3} , \underline{a}^{U15} , and \underline{a}^{U18} show full male and female viability and transmission. \underline{A}^{It} is also fully viable in male and female gametophytes and regular in transmission.

(3) Relation to \underline{Dt} . The reaction to \underline{Dt} is determined chiefly by examination of the aleurone of seeds produced by the cross $\underline{a}^{mutant}/\underline{a}^P \underline{Dt} \underline{Dt} \times \underline{a}^{dotless} \underline{Dt} \underline{Dt}$ in comparison with sister ears of $\underline{a} \underline{a}^P \underline{Dt} \underline{Dt}$ similarly pollinated. Supplementary determinations have been made in other ways.

None of the mutants show regular dotting comparable to that of \underline{a} . Occasional seeds may show a single dot, but this may be ascribed to the $\underline{a}^{dotless}$ tester as well as to the \underline{a}^{mutant} . Evidence on dotting in the homozygous $\underline{a}^{mutant} \underline{Dt}$ combination is still scanty and has shown no dots so far.

L. J. Stadler, J. W. Cameron, K. O. DeBoer,
Herschel Roman

University of Puerto Rico, Rio Piedras, Puerto Rico

Although I am concerned primarily with corn breeding, I have started genetical studies of corn grown in Puerto Rico. There are many mutants found in local corn, such as white and yellow seedlings, various other chlorophyll deficiencies, male and female sterility, narrow leaf, tassel seeds, vivipary, brown midrib, red pericarp, variegated pericarp, and others. Whether these mutants have been introduced from the North, and subsequently incorporated into local corn, or are local in origin it is difficult to tell with certainty. However, it is well known that corn from the mainland is not adaptable to local conditions, and the few attempts to

introduce it to Puerto Rico have failed. The corn imported from other regions, such as Santo Domingo, Cuba and Argentine is used exclusively for feed.

Many crosses were made between some of these mutants and unrelated stocks, and F_2 's and backcrosses are expected to be raised this spring. For the present I want to mention two interesting cases: brown midrib and tassels, and forked or split stem.

Brown midrib and tassels. The F_1 data suggest that we have a new dominant mutant, tentatively designated Bm-b, for the development of brown pigment in midrib and tassels. The color appears rather late, before tasseling, and varies in intensity especially in tassels, sometimes approaching color of tassels of a B Pl plants.

This mutant was found in one of the inbred lines. Bm-b plants were selfed and crossed to three unrelated stocks. The selfed plants had also red pericarp and cob. The five F_1 crosses segregated in the following ratio:

<u>Bm-b</u> <u>P^{VV}</u>	<u>Bm-b</u> <u>p</u>	<u>bm-b</u> <u>P^{VV}</u>	<u>bm-b</u> <u>p</u>
193	2	0	183

The result suggests that Bm-b is closely linked with P. The presence of the red pericarp in Bm-b plants, as well as the development of anthocyanin in seedlings of all F_1 plants indicate that the development of brown color in tassels and midrib is not due to a. Also there is evidence that we are dealing with red and not cherry pericarp, as there is no Pl involved in these crosses.

Forked or split stem. A number of plants were observed in several cultures in which the stem is split or forked. The forking may occur in any node. If forking takes place at the node below the ear, then two ears and tassels are formed.

From two selfed forked ears 44 plants were raised, all of which were normal, non forked. The F_1 between forked and normal plants yielded:

	<u>Normal</u>	<u>Forked</u>
	153	2
	22	2
	26	0
	<u>15</u>	<u>1</u>
Total	216	5

G. A. Lebedeff

IV. Miscellaneous Co-op Items

1. Co-op stocks. An effort is being made to grow each stock in our collection at least once every three years. To maintain vigor, especially in the naturally weaker stocks, we shall follow a practice started a few years ago. The co-op stocks are crossed with standard inbreds I (U.S. No. 204) and II (West Branch). The desired characters are then recovered from each of these hybrids, and crosses are then made between these desired sorts from the two sources.

2. Assignments of chromosomes for mapping. In News Letter 13, April 15, 1939, page 39, there is given a list of persons who are mainly responsible for linkage studies on the different chromosomes, and for the building up of linkage stocks. At the Christmas meetings in 1940, this list was examined by the co-operators present, and a few changes were made. The revised assignments follow:

Chromosome 1	-	Emerson
Chromosome 2	-	Rhoades and Clokey
Chromosome 3	-	Brink and Woodworth
Chromosome 4	-	Singleton and Brunson
Chromosome 5	-	Burnham and Cartledge
Chromosome 6	-	Burnham, Lebedeff and Stadler
Chromosome 7	-	Jenkins and Fraser
Chromosome 8	-	Sprague and Perry
Chromosome 9	-	Shafer and Eyster
Chromosome 10	-	Lindstrom

3. Personals.

(a) Carlos A Krug of Sao Paulo, Brazil, is spending a year in this country, with the special purpose of studying the genetics and cytology of citrus, at Riverside, California. Krug brought to the U.S.A., 60 types of maize collected by his assistant in Bolivia, Peru, Ecuador, and Columbia. These have been added to the Co-op stocks. Small amounts of seed can be spared to cooperators who are especially interested.

(b) D. G. Langham of Venezuela is in this country for a few months, for the purpose of collecting corn and of working on a special problem in connection with his research.

(c) Two of our number, M. M. Rhoades and B. McClintock, will be at Cold Spring Harbor this summer, along with Muller, Wright, Nebel and other geneticists.

(d) R. A. Emerson left Ithaca early in February for a six-weeks vacation in Florida.

V. Maize Publications

Since the preparation of the list of publications in News Letter 14, March 5, 1940, the following articles have appeared in print:-

Anderson, E. G. and Brink, R. A. - Translocations in maize involving chromosome 3. Genetics 25: 299-309, 1940.

Andres, J. M. - Analisis genetico del color de endosperma en algunos maices comerciales Argentinos. Inst. Genet. Univ. Buenos Aires vol. 1: 25 p., 1939.

Avery, G. S., Jr., Creighton, H. B. and Shalucha, B. - Extraction methods in relation to hormone content of maize endosperms. Amer. Journ. Bot. 27: 289-300. 1940.

Beard, D. F. - Relative values of unrelated single crosses and an open-pollinated variety as testers of inbred lines of corn. Abstr. Ph.D. thesis, Ohio State Univ. 33: 9-18, 1940. (Includes discussion of susceptibility to Diplodia Zeae).

Bercaw, L. O., Hannay, A. M. and Larson, N. G. - Corn in the development of the civilization of the Americas. A selected and annotated bibliography. U.S.D.A. Agr. Econ. Bibl. 37: 195 p., 1940.

Bonnett, O. T. - Development of the staminate and pistillate inflorescences of sweet corn. Journ. Agr. Res. 60: 25-37, 1940.

Borgeson, C. and Hayes, H. K. - The Minnesota method of seed increase and seed registration for hybrid corn. Journ. Amer. Soc. Agron. 33: 70-74, 1941.

Buss, H. - Die Problemstellung in der deutschen Maiszüchtung. Deut. Land. Presse. 67: 87, 1940.

Capinpin, J. M. and Rollan, A. O. - Hybrid vigor in the first generation crosses between strains of Cebu corn. Philipp. Agr. 28: 491-503, 1939.

Carnegie Institute Washington - Maize cultivation in northwestern Guatemala. (Compiled from data collected in the field by Raymond Stadelman). Carnegie Inst. Wash. Pub. 523: 83-263. 8 pl. map, 1940. Processed.

- Clark, F. J., and Copeland, F. C. - Chromosome aberrations in the endosperm of maize. Amer. Journ. Bot. 27: 247-251, 1940.
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- Gini, E. - Estudios sobre esterilidad en maices regionales de la Argentina. Anales Inst. Fitotecn. Santa Catalina (La Plata, Arg.). 1: 135-158, 1940. (Eng. Sum.)
- Graner, E. do A. - Variacoes do valor de "linkage". Revista Agr. (Piracicaba) 15: 168-175, 1940. (Eng. Sum.)
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- Heyne, E. G. and Brunson, A. M. - Genetic studies of heat and drought tolerance in maize. Journ. Amer. Soc. Agron. 32: 803-814, 1940.
- Hirschhorn, E. and Hirschhorn, J. - Accion del pH sobre los caracteres culturales del carbon del maíz. Ustilago Zeae (Beck) Ung. Physis (Buenos Aires) 18: 223-251, 1939.

- Hoerner, I. R., and Snelling, R. O. - Effect of pollination upon chemical composition of silks of certain inbred lines of maize. Journ. Amer. Soc. Agron. 32: 213-215, 1940.
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Papers in Press

Longley, A. E. - Knob positions on teosinte chromosomes.
Journ. Agr. Res.

_____ - Chromosome morphology in maize and its
relatives. (A review). Submitted to Botanical
Review, but not yet accepted.

Saboe, L. C. and Hayes, H. K. - Genetic studies of smut
reactions in maize by means of chromosomal trans-
locations - Submitted to Journ. Amer. Soc. Agron.

VI. New Genes

1. Five alleles of a for aleurone color. No symbols given as yet. See contribution by M. M. Rhoades, Columbia University, item 2.
2. A new member of the r series for aleurone color. See report by M. M. Rhoades, item 5.
3. New gene for pollen abortion pa contribution of C. R. Burnham, item 1. —
4. An R^{ch} allele of R contribution of E. G. Anderson, item 1.
5. Mutations produced by irradiation. See contribution by L. J. Stadler and co-workers.
6. Bm- b- brown midrib and tassel. Contribution of Lebedeff from Univ. of Puerto Rico.

MAIZE GENETICS COOPERATION

NEWS LETTER

16

1942

The data presented here are not to be used in
publications without the consent of the authors.

Department of Plant Breeding
Cornell University
Ithaca, N. Y.

MAIZE GENETICS COÖPERATION
DEPARTMENT OF PLANT BREEDING
CORNELL UNIVERSITY
ITHACA, NEW YORK

December 10, 1941

To Maize Geneticists:

Circumstances beyond the control of mortal man have again laid Maize Genetic Cooperation on my doorstep. It is, of course, too early to know what can be done next summer by any of us. But I feel that such fundamental and long-time undertakings as ours should not be lightly abandoned. I plan, therefore, to assemble material for a Maize Genetics News Letter to be mailed on or about the first of February next. Since I shall be away from my office during much of February and March, I must have your reports by January 15. Even if you cannot make a complete report by that time, please send me whatever you can get ready.

Sincerely,

R. A. Emerson

R. A. Emerson

RAE:P

[Feb 10, 1942]

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I. PROFESSOR A. C. FRASER

Somewhat more than a year ago, when I expected to retire at the end of June, I persuaded Professor Fraser to take charge of Maize Genetics Coöperation. I did not retire, and now Professor Fraser has gone. He assembled the material for the 15th News Letter. It was done in his characteristically careful way. It has pleased me a lot to hear more than one of you say that last year's News Letter was the best one so far put out.

Without the knowledge of any of us, Professor Fraser had been treated by a specialist for over a year. He did not meet his class in advanced genetics after the spring vacation, but he did prepare seed for planting and staked glossy seedlings in the field. Dr. Murray and I made pollinations for him in the summer and Dr. Murray made the final records from his cultures. Some of these are reported in this News Letter.

Professor Fraser was primarily a teacher. He was unusually successful with both undergraduate and graduate students. Many of you, who had courses with him, have told me this and more. You who were thus associated with him for a few years will feel this loss. To those of us who had been his colleagues for many years, his death came as a profound shock. Our memory of many things about him is small consolation. His ability, his determination, his untiring energy and resourcefulness, his never failing cheerfulness - he "kept his chin up" to the end - his willing helpfulness, and withal his unassuming manner, all these memories of him force upon all of us an ever growing sense of our loss.

R. A. Emerson

II. REPORTS FROM COÖPERATORS

The presentation of data in these News Letters is not regarded as constituting publication. These data should not, therefore, be used in published papers without the consent of the authors.

R. A. Emerson

Columbia University, New York City

1. Location of Dt in the short arm of chromosome 9. - F_2 data presented in the 1941 News Letter indicate that Dt is situated close to the yg2 locus at the end of the short arm of chromosome 9. These data also suggested that Dt was about ten units beyond yg2. However, Creighton found only one percent recombination between yg2 and the terminal knob. Backcross tests recently completed prove that Dt does lie approximately seven units beyond yg2. The low recombination value of one percent for the yg2-knob region may be ascribed to the disturbing effect on crossing over of the large heterozygous knob present in Creighton's set-up. The backcross data are as follows:

$\frac{Dt}{+} \frac{+}{yg2} \frac{+}{sh} \frac{+}{wx}$									
<u>0</u>	<u>1</u>	<u>2</u>	<u>3</u>	<u>1-2</u>	<u>2-3</u>	<u>1-3</u>	<u>Total</u>		
333 278	22 23	76 86	82 64	0 3	2 3	0 0			
611	45	162	146	3	5	0	972		
<u>Dt-Yg2</u> 5.2%		<u>Yg-Sh</u> 17.4%		<u>Sh-Wx</u> 15.8%					

$\frac{Dt}{+} \frac{+}{yg2} \frac{+}{sh}$					
<u>0</u>	<u>1</u>	<u>2</u>	<u>1-2</u>	<u>Total</u>	
306 228	18 33	83 93	2 4		
534	51	176	6	767	
<u>Dt-Yg2</u> 7.4%		<u>Yg2-Sh</u> 23.7%			

	<u>Dt+</u>	<u>Dt yg2</u>	<u>++</u>	<u>+yg2</u>	<u>Total</u>
$\frac{Dt}{+} \frac{+}{yg2}$	283	24	25	293	625
<u>Dt-Yg2</u> 7.8%					

$\frac{Dt}{+} \frac{+}{sh} \frac{+}{wx}$							
<u>0</u>		<u>1</u>		<u>2</u>		<u>1-2</u>	<u>Total</u>
345	330	115	110	85	76	3	4
675		225		161		7	1068
<u>Dt-Sh</u> 21.7%				<u>Sh-Wx</u> 15.7%			

	<u>Dt+</u>	<u>Dt sh</u>	<u>++</u>	<u>+sh</u>	<u>Total</u>
$\frac{Dt}{+} \frac{+}{sh}$	838	277	324	765	2204
	<u>Dt Sh</u> 27.3%				

2. In a culture with A B Pl and A b Pl plants the R^r and R^g? alleles were segregating. A b Pl R^g? plants had green anthers with colored glumes. There was no color at the base of the culm but an occasional small blotch of color was found along the culm. Possibly a new R allele.

3. Jenkins gave the writer a selfed ear of inbred Hy that was segregating for what appeared to be a green seedling character. This new recessive mutant is linked with either C or R. Inasmuch as A B pl plants homozygous for this gene have a deep bronze color instead of the usual red, this gene has been tentatively designated "bronze" (symbol bz). A b pl and A b Pl plants homozygous for bz are not green but have a bronze color at the base of the culm. Some strains of A b pl and A b Pl plants homozygous for bz have chocolate colored anthers while other strains have green anthers. Some interactions with the R alleles may be involved here. The effect of bz on the color of A B Pl plants or on pericarp color has not yet been determined. The effect of bz on aleurone color is also unknown since it arose in a line homozygous for recessive c and r and its being linked to one of these factors makes the aleurone effect difficult to determine. The bz gene has a rather remarkable pleiotropic effect. In addition to affecting the anthocyanin system it also causes considerable pollen abortion. The sterility effect of bz is variable from season to season. At Arlington, Virginia in the summer of 1940 the amount of aborted pollen was so great that the anthers were shriveled and many failed to dehisce while in the summer of 1941 at Cold Spring Harbor little or no pollen abortion was evident.

4. Location of dwarf-7. Singh reported that d7 belonged in the tenth linkage group approximately 27 units to the right of R. Singh's placement of d7 rested upon the linkage of d7 with aleurone color in F₂ populations segregating for both C and R, and upon an F₂ population of 109 individuals segregating for d7 and golden-1 where he found 35 percent recombination

between d7 and g. Singh's placing of d7 in chromosome 10 rests entirely upon the loose and dubious linkage of d7 with g. The writer has been unable to find linkage of d7 with genes in chromosome 10. F_2 data from cultures segregating for d7 and shrunk show 24 percent recombination. Apparently d7 belongs in chromosome 9 and since d3 shows 25 percent recombination with sh it is not unlikely that d7 and d3 are identical. At any rate it is clear that the d7 locus should be dropped from the map of the tenth linkage group.

5. Inasmuch as the writer was assigned chromosome 2 he has from time to time collected additional data on the location of certain genes placed in the map by two-point tests. The floury locus was placed between sk and ts by two-point data. This has been confirmed by three-point tests. Some of the data involving floury are presented below:

$$\frac{lg \ g1 \ B \ Fl \ v4}{Lg \ G1 \ b \ fl \ V4} \quad x \quad lg \ g1 \ b \ V4 \ v4$$

B.C. for lg g1 B Fl F_2 for V4

Lg-G1 16%; G1-B 16%; B-Fl 16%; Fl-V4 14%; B-V4 23%

The order is lg g1 B Fl V4

$$\frac{B \ Fl \ ts \ v4}{b \ fl \ Ts \ V4} \quad x \quad b \ \frac{Ts-v4}{ts-V4}$$

B.C. for B Fl F_2 for ts and v4

B-Fl 19%; Fl-Ts 3%; B-Ts 21%; Fl-V4 18%; B-V4 32%

The order is B Fl ts v4

Summary of unpublished linkage data for chromosome 2

XY Genes	Phase	XY	Xy	xY	xy	Total	Percent recombination
B Fl	CB	549	135	129	663	1476	18
B Ts	RS	254	101	413	27	795	21
B V4	RS	480	204	716	76	1476	26
Fl Ts	RS	376	243	768	7	1394	3
Fl V4	RS	569	281	891	60	1801	18
Gs2 Fl	RS	161	212	113	19	505	17

M. M. Rhoades

6. The following experiment was undertaken to determine if the pollen tubes obtain nutriment from the silks as they grow downward or whether food materials stored in the pollen grains are the chief source of energy.

Pollinations were made one day after cutting back the silks, so that brushes of silks approximately $1\frac{1}{2}$ inches long were available. Following pollination that portion of the silk (with the attached pollen grains) extending beyond the husks was cut off at intervals of $\frac{1}{2}$, $\frac{3}{4}$, 1, $1\frac{1}{2}$, 2, $2\frac{1}{2}$, 3, $3\frac{1}{2}$, 4, and 6 hours after pollinating. Silks removed at different intervals of time were fixed in alcohol and later stained with carmine-chloral hydrate.

It was found that germination occurred within the first half-hour. Germinated grains on silks removed at the different time intervals were examined cytologically to determine whether or not the two sperm cells and the tube nucleus had passed into the silk. The data are given as follows:

Table 1. Percent of germinated grains with no (0), one (1), and two (2) sperm nuclei, and having (1) or lacking (0) a tube nucleus on silks removed at different time intervals after pollination.

Hours	:2 sperm:	:	:	:	:	:	:	:	No. of
after	:cells :	:	:	:	:	:	:	:	grains
pollin-	:1 tube :2 sperm:1 sperm:1 sperm:0 sperm:0 sperm:	:	:	:	:	:	:	:	examin-
ation	:nucleus:0 tube :1 tube :0 tube :1 tube :0 tube :	:	:	:	:	:	:	:	ed
$\frac{1}{2}$: 92 :	0 :	0 :	0 :	6 :	2 :	50 :		
$\frac{3}{4}$: 80 :	4 :	4 :	0 :	12 :	0 :	25 :		
1	: 82 :	0 :	0 :	2 :	7 :	9 :	52 :		
$1\frac{1}{2}$: 59 :	1 :	1 :	0 :	20 :	18 :	61 :		
2	: 17 :	2 :	2 :	1 :	9 :	69 :	120 :		
$2\frac{1}{2}$: 0 :	0 :	0 :	0 :	5 :	95 :	20 :		
	: :	:	:	:	:	:	:		

The average number of grains on each examined silk was approximately twenty but considerable variation was found. Every silk examined, however, had a number of established grains.

Most of the sperm and tube nuclei pass out of the pollen grains between one and two hours after pollination. The sperm cells usually precede the tube nucleus in passing into the pollen tube. Four hours after pollination the pollen grains are nearly empty. The pollen grains retained a considerable portion of their contents two hours after pollination, even though the sperm nuclei and the tube nucleus had entered the silk. Pollen grains cut off before all of the food reserves had passed into the pollen tubes might not achieve fertilization for lack of sufficient nutriment if the growing tubes obtain little or no nourishment from the stylar tissue. The pollen tubes would contain the sperm and tube nuclei, but only part of the total food material stored in the pollen. If the pollen tubes obtained nutriment from the silk, they would continue to grow and all the ovaries would be fertilized.

If, however, the pollen tube could not obtain sufficient

nutriment from the silk, it would grow only until the available food material in the pollen tube was exhausted. Many of the ovaries at the bottom of the ear would not be fertilized, because the pollen tubes lacked the energy to grow a longer distance.

Seed set was determined at maturity.

Table 2. Number of ears, total number of seeds, and the percent of seeds found in the upper half of all the ears of corn for each time interval.

Series A	Hours after pollination						
	: 1	: 2	: 2½	: 3	: 3½	: 4	: 6
Number of ears	: 3	: 6	: 5	: 6	: 9	: 10	: 4
Total no. of seeds	: 1	: 193	: 862	: 337	: 1233	: 2607	: 1380
Percent seeds in upper half	: -	: 64	: 71	: 75	: 72	: 58	: 52

Series B	Hours after pollination				
	: 1	: 2	: 3	: 4	: ∞
Number of ears	: 8	: 8	: 8	: 7	: 11
Total no. of seeds	: 5	: 26	: 81	: 408	: 3182
Percent seeds in upper half	: -	: 78	: 69	: 68	: 52

(Note: ∞ = silks were not removed)

The number of seeds in the upper half of the ear was consistently greater than in the lower half at the time intervals when food material still remained in the pollen grain at the time of removal. Inasmuch as nearly all of the contents of the pollen grain had been discharged into the pollen tube by four hours after pollination but there were an appreciable number of unfertilized ovules at the base of the ear it seems that practically all of the stored reserves are needed for the long journey to the basal ovules. It is doubtful if the stylar tissue offers any nourishment to the growing pollen tube.

Sidney Wiesner

Connecticut Agricultural Experiment Station
New Haven, Connecticut

1. Paired red and dark purple mosaic areas in light purple seeds, heterozygous for Pr pr pr, rarely show growth changes. In some of these cases the red area grows out beyond the normal cells, sometimes the dark area. In the few cases that have been examined so far no growth changes accompany the exchange of both Pr and Bt. Since Bt is close to the centromere, presumably, paired changes that include Pr and Bt involve an exchange of almost the entire right arm of chromosome 5. If the alteration in growth were due to a loss or accumulation of specific growth regulating genes or to a general chromosome

unbalance it would be expected that all of the paired changes involving both Bt and Pr would be altered. Since they are not, this is a strong indication that growth changes result from breaks and reattachments at critical places in the chromosomes.

2. Paired pericarp mosaics, especially those that may occur in plants heterozygous for p^{RW} and p^{WR} , would make possible a distinction between reciprocal translocation and somatic crossing over. In plants of this composition red-seeded, red-cobbed ears would show colorless seeds underlaid with red cob adjacent to colored seeds over white cob. Any mosaics of this type should be examined cytologically and put on record. The writer would appreciate having any of these mosaics, especially where the areas involved cover several seeds.

D. F. Jones

3. Effect of environment on aleurone color - Marcross sweet corn with the aleurone constitution A C r Pr was changed to a purple aleurone (phenotype A C R Pr) by growing in the greenhouse in the winter time with no additional light. The corn was planted on January 21, 1941 in soil fertility plots where different types of phosphorous fertilizers were being tested. The fertility in all plots was sufficient to produce a normal crop of corn. In some cases ears were produced in the tassels as is characteristic of corn grown in this latitude with no extra light. Many fully purple kernels were found on the main ears as well as those produced in the tassel. One tassel ear had all the kernels fully colored similar to any A C R Pr stock. Examination showed this color to be in the aleurone layer. Seeds from the fully colored tassel-ear were planted in the field in the summer of 1941. Three selfed ears showed no aleurone color. The kernels were all Y su. Ears crossed by A C R Pr were entirely purple, also those crossed by a C R pr and A c R. Ears crossed by ACr were colorless showing the aleurone constitution to be A C r Pr. No explanation is readily available for the apparent changing of r or R when grown in the greenhouse. The experiment is being repeated in the greenhouse in 1942.

W. R. Singleton

4. In a field corn test in 1938, 311 different hybrids and inbreds were grown. A total of 14,916 ears were picked and of this number 26 (from 22 different lines) were classified as semi-sterile. This is not a good determination of the frequency of changes giving semi-sterility, but is an indication of the types of changes that occur. Progeny of 24 of the 26 ears have been grown for one to three generations to test the transmissibility of these sterilities. Twelve were definitely transmitted, three had questionable transmission and nine were not transmitted and were probably due to environmental or physiological causes. Nine of the twelve have been examined cytologically, and in these the following changes were found:

asynapsis, a 1-6 translocation, a 6-8 translocation, a pollen lethal character with no apparent chromosomal change or deficiency, and a long inversion in chromosome 1 including the centromere. It is of particular interest that the inversion in chromosome 1 was found in three different hybrids having as one parent, the inbred U.S. 4-8. It would be desirable to know if 4-8 has been found to have this inversion in the heterozygous condition and whether any unusual number of semi-sterile ears have been found in hybrids with 4-8. The 4-8 inbred used in the hybrids grown in Connecticut was not homozygous for the inversion since all the ears were not semi-sterile. It could have been obtained by contamination, but it seems unlikely that three hybrids with one parent in common would have been so affected. The inversions are apparently the same cytologically although crosses between them have not been made as yet to detect any differences.

Twelve semi-sterile ears, obtained from other field corn tests and sweet corn trials, have been tested for transmissibility. Five were not transmitted, one possibly is transmitted and six were transmitted. From the last six a lethal ovule character was found, a 2-5 translocation and a 6-9 translocation. Three have not been examined cytologically.

5. An unusual example of a somatic change was found in a plant heterozygous for the translocation T5-9a. The ear on this plant had approximately half the silks green and half red. Other plants from the same cross had green silks, with the exception of two plants having a few red silks and all others green. Although the ear which was about half red and half green was open pollinated, tests are being made to determine if the change was only in maternal tissue.

F. J. Clark

Cornell University, Ithaca, N. Y.

1. White-capped red pericarp - E. G. Anderson reported (Genetics 9:442-453. 1924) an allelic series of maize pericarp and cob colors with their genes at the locus of P. These included self red pericarp with red cob R-R (Anderson's symbols are used here, the first letter representing pericarp and the second cob color), colorless pericarp with red cob W-R, colorless pericarp with white cob W-W, variegated pericarp and cob V-V, mosaic pericarp and cob M-M, white-capped red pericarp with red cob C-R, and white-capped red pericarp with white cob C-W. That these combinations of pericarp and cob colors constitute an allelic series has not been questioned heretofore, so far as I am aware, and is not now questioned except for C-R and C-W. In fact, all the data with which I am familiar tend to substantiate Anderson's conclusions except for white-capped red pericarp. Heretofore I have regarded C-R and C-W as belonging to the P series of alleles and long ago (Nebr. Agr. Exp. Sta. Rpt. 24: 57-90. 1911) published records for C-W -

involving exceedingly few individuals - in support of this idea. Anderson's records involved adequate numbers. For the backcross (C-W x W-R) x W-W, the two parental types only were obtained, 1684 C-W and 1751 W-R. But he reported that: "This cross is not wholly satisfactory, since heterozygous C-W is light colored, making immature ears difficult to separate from white." He found no red-cobbed ears with white-capped red pericarp, while the white-cobbed ones all exhibited this pericarp color. But, in his description of W-R, he said: "Pericarp white (colorless) in some varieties, pale orange in others."

If these statements seem to imply that both Anderson and I were wrong in our early interpretations respecting C-W, I must admit that I have no evidence to support such an implication. But for C-R I shall here present evidence which indicates that the white-capped red pericarp of Bloody Butcher is conditioned by multiple genes. The C-W combination studied earlier by Anderson and by me is that seen in Northwestern Dent. The color patterns of the pericarp of these two varieties are identical in appearance and the intensity of pigment of both is reduced noticeably when made heterozygous by crossing with colorless pericarp types. In this respect both differ from self-red, variegated red, and mosaic red. It seems strange, therefore, that white-capped red of Northwestern Dent, C-W, should differ in inheritance from the apparently identical pericarp color of Bloody Butcher, C-R. Both Anderson (1924) and I (1911) reported crosses of C-W x W-R and of most of the other possible combinations of pericarp and cob color patterns, but neither one of us reported results of C-R x W-W.

All the crosses to be reported here involve a single one of Dr. Wiggans' inbred strains of Bloody Butcher (C-R), his inbred #4. This was crossed with three others of his inbreds; namely, Cornell 11 inbred #3 (W-R), Luce's Favorite inbred #1 (W-W) and Onondaga White inbred #2 (W-W). Generations F₂ and F₃ and repeated backcrosses to W-W have been studied. Since in one of the crosses, C-R x W-R, white cob color is not involved, both parents having red cobs, I shall present first the evidence involving pericarp color alone from all the crosses. In the presentation to follow the intensity of pericarp color is indicated in six grades. Grade 0 indicates pericarp in which no tinge of color can be seen, grade 6 the color intensity of the Bloody Butcher parent, grade 5 that of most F₁ ears, grade 1 a barely discernible tinge of color and 2, 3, 4 intermediate grades, in ascending order of color intensity. The mean grade of color intensity is presented both for all ears and for ears with some color in the pericarp. In table 1 are given the records of nine different F₂ cultures of the three crosses and of nine backcrosses of F₁ to colorless pericarp.

Table 1

Gen-:	:	Progeny grades							:	Mean grade	
era-:Parent:	:								:	Total:	All :Colored
tion:grades:	:	0	1	2	3	4	5	6	:	ears:	ears
F ₂	: 5 :	103	9	76	114	117	159	18	:	596	:3.1 : 3.8
bc	: 5 x 0 :	273	13	74	113	114	54	0	:	643	:1.9 : 3.3

The ratio of plants with colored to those with colorless pericarp is 4.8 : 1 for F₂ and 1.4 : 1 for backcrosses instead of 3 : 1 and 1 : 1, respectively. The frequency distributions of individuals of grades 1 to 6 are those typical of multiple-gene inheritance. The mode and the mean grade are somewhat lower in the backcross than in F₂, just as F₁ is of lower grade than the colored parent.

Progenies of selfed F₂ and of selfed backcross plants with diverse grades of pericarp color are recorded in table 2.

Table 2

Number :	:	Progeny grades							:	Mean grades	
of :Parent:	:								:	Total:	All :Colored
cultures:grade :	:	0	1	2	3	4	5	6	:	ears:	ears
4	: 0 :	104	-	-	-	-	-	-	:	104	: 0 :
2	: 0? :	35	12	-	-	-	-	-	:	47	:0.3 : 1.0
14	: 1 :	171	227	38	-	-	-	-	:	446	:0.7 : 1.1
5	: 2 :	29	58	43	20	8	4	-	:	162	:1.5 : 1.9
7	: 3 :	46	28	46	65	38	9	-	:	232	:2.2 : 2.7
3	: 4 :	19	8	10	17	28	16	-	:	98	:2.8 : 3.4
3	: 5 :	-	1	2	9	26	48	23	:	109	:4.7 : 4.7
2	: 6 :	-	-	1	1	9	35	32	:	78	:5.2 : 5.2

Individuals of various pericarp-color grades of the first backcross generation were backcrossed a second or third time. The progenies of these backcrosses are reported in table 3.

Table 3

Number :	:	Progeny grades							:	Mean grades	
of :Parent:	:								:	Total:	All :Colored
cultures:grades:	:	0	1	2	3	4	5	6	:	ears:	ears
5	: 0 x 0 :	206	-	-	-	-	-	-	:	206	: 0 :
1	: 0? x 0 :	74	4	-	-	-	-	-	:	78	:0.05 : 1.0
4	: 1 x 0 :	65	63	-	-	-	-	-	:	128	:0.5 : 1.0
4	: 2 x 0 :	59	20	64	9	-	-	-	:	152	:1.2 : 1.9
1	: 3 x 0 :	35	-	13	13	-	-	-	:	61	:1.1 : 2.3
6	: 4 x 0 :	46	34	35	42	19	2	1	:	179	:1.8 : 2.4
1	: 5 x 0 :	38	-	-	5	40	7	-	:	90	:2.3 : 4.0

Tables 2 and 3 not only exhibit frequency distributions characteristic of multiple-gene inheritance, but also demon-

strate that selection is effective in isolating diverse types, as in most instances of quantitative inheritance.

In many of the crosses reported above, cob color, as well as pericarp color, was involved. In table 4 the data for F_2 and the first backcross generations are presented for red-cob and white-cob ears separately.

Table 4

Gen-:		Progenies								Mean grades	
era-:	Parent:	Cob :	Grades								Total:
tion:	grades:	color:	0	1	2	3	4	5	6	:	All : Colored
											ears: ears
F_2	5	(R	32	4	45	58	72	113	17	:	341 : 3.6
		(W	49	4	24	25	13	3	-	:	118 : 1.6
bc	5 x 0	(R	48	6	38	41	40	37	2	:	212 : 2.7
		(W	119	2	7	41	28	5	-	:	202 : 1.4

The segregation of cob colors was sharp without appreciable intergrades between red and white. The ratios of red-cob to white-cob ears, 341 : 118 and 212 : 202 in the F_2 and backcross generations, respectively, are approximately the 3 : 1 and 1 : 1 ratios expected where a single gene pair is concerned. The mean grades for pericarp color were somewhat higher in the red-cob than in the white-cob lots. This is the more pronounced when mean grade is calculated from all ears, because a higher percentage of the white-cob ears have colorless pericarp than is true of red-cob ears.

From the cross C-R x W-W, there have been obtained the four combinations; namely, C-R, W-R, C-W, W-W, expected on the basis of independent inheritance of pericarp and cob colors. The numerical relations, however, do not fit those of independent inheritance - 9-3-3-1 and 1-1-1-1 - as indicated in table 5.

Table 5

		C-R	W-R	C-W	W-W	Total
F_2	Observed	309	32	69	49	459
	Calculated	258	86	86	29	459
bc	Observed	164	48	83	119	414
	Calculated	103.5	103.5	103.5	103.5	414

If we were dealing with dihybrid inheritance, these data would indicate linkage of pericarp and cob colors with 26% or 31% of crossing over for F_2 or backcross progenies, respectively. It is conceivable that there is one primary gene for white-capped red pericarp which is modified in its expression by other genes.

Records of F_3 , and of F_2 after one or more backcrosses, are summarized in table 6.

Table 6												
Number of cultures	Parent grade	Cob color	Progeny Grades								Mean grades	
			0	1	2	3	4	5	6	Total	All ears	Colored ears
1	0	(R	22	-	-	-	-	-	-	22	0	
		(W	14	-	-	-	-	-	-	14	0	
5	1	(R	27	94	35	-	-	-	-	156	1.1	1.3
		(W	31	3	-	-	-	-	-	34	0.1	1.0
2	2	(R	7	40	13	2	-	-	-	62	1.2	1.3
		(W	12	3	-	-	-	-	-	15	0.2	1.0
3	3	(R	16	12	16	25	17	3	-	89	2.3	2.8
		(W	7	2	4	4	4	-	-	21	1.8	2.7
1	3	(R	3	10	7	11	1	-	-	32	1.9	2.1
		(W	11	-	-	-	-	-	-	11	0	
5	4	(R	16	12	7	17	44	24	-	120	3.1	3.6
		(W	9	2	3	12	10	4	-	40	2.6	3.4

Individuals of various pericarp-color grades among backcross and F_2 progenies were backcrossed to W-W, with the results shown in table 7.

Table 7												
Number of cultures	Parent grades	Cob color	Progenies Pericarp grade								Mean grades	
			0	1	2	3	4	5	6	Total	All ears	Colored ears
2	0 x 0	(R	79	-	-	-	-	-	-	79	0	
		(W	74	-	-	-	-	-	-	74	0	
3	1 x 0	(R	2	91	-	-	-	-	-	93	1.0	1.0
		(W	80	-	-	-	-	-	-	80	0	
1	1 x 0	(R	7	8	-	-	-	-	-	15	0.5	1.0
		(W	17	8	-	-	-	-	-	25	0.3	1.0
1	2 x 0	(R	8	7	7	1	-	-	-	23	1.0	1.6
		(W	20	-	-	-	-	-	-	20	0	
6	4 x 0	(R	38	38	9	17	20	17	-	139	2.0	2.7
		(W	39	8	19	13	11	15	-	105	1.9	3.1

Tables 6 and 7 show at least that low grade pericarp color is closely linked with red cob color. That even this very low grade pericarp color cannot be allelic to cob color is shown by the occurrence of cultures in which the red-cob ears, as well as

the white-cob ones, exhibit no discernible trace of pericarp color.

In addition to the cultures that segregated for cob color, there occurred, in F_3 and backcross generations of the cross C-R x W-W, progenies³ that bred true for red or for white cob color, as shown in table 8.

Table 8

Number of cultures	Parent grades	Cob color	Progenies Pericarp grade								Mean grades	
			0	1	2	3	4	5	6	Total	All ears	Colored ears
1	1	R	15	23	-	-	-	-	-	38	0.6	1.0
2	1	W	18	15	-	-	-	-	-	33	0.5	1.0
3	2	W	10	15	30	18	8	4	-	85	2.1	2.4
3	3	W	9	4	19	25	16	6	-	79	2.7	3.0
1	5	R	-	1	2	5	7	11	11	37	4.3	4.3
1	5	W	-	-	-	3	12	11	1	27	4.4	4.4
2	6	R	-	-	1	1	9	35	32	78	5.2	5.2
6	0 x 0	W	197	-	-	-	-	-	-	197	0	0
7	1 x 0	W	66	73	2	-	-	-	-	141	0.5	1.0
1	2 x 0	W	5	4	16	6	-	-	-	31	1.7	2.1
3	3 x 0	W	86	2	27	28	17	1	-	161	1.3	2.8
3	4 x 0	W	24	12	15	28	7	-	-	86	1.8	2.5

It will be noted from table 8 that six cultures produced nothing but W-W ears like one parent of the original cross; that three cultures produced only C-R ears like the other parent but with considerable variation in intensity of pericarp color; that one culture had only C-W ears like Northwestern Dent but with some variation in pericarp color intensity; that, while no true breeding W-R lots have been obtained, two cultures (table 7) contained only W-R and W-W ears, from which homozygous W-R stocks can presumably be obtained.

From all this it seems obvious that white-capped red pericarp of Bloody Butcher is not a member of the P allelic series but is conditioned by multiple genes one or more of which are linked with red cob and therefore with P. So far as the P allelic series is concerned, Bloody Butcher is apparently W-R to which has been added other genes for pericarp color not of that series.

Since white-capped red pericarp of Northwestern Dent is identical with that of Bloody Butcher in appearance and in having its intensity reduced in the heterozygous condition, it will be interesting to discover whether Anderson and I were wrong in our earlier interpretation and, if then right, what relation exists between C-W of Northwestern Dent and the C-W that has come from the cross of C-R x W-W. The study is underway.

R. A. Emerson

2. Linkage data involving an and Ts₃ or Ts₆ - Striking differences between complementary crossover classes were reported by Emerson 1941 News Letter (p. 13-15). These records may not have been wholly accurate for the following reason. Some of the Ts plants failed to develop ears since the tassels were not removed at the time of emergence. Classification of an from the tassel when combined with Ts is difficult. Therefore, similar progenies were repeated this summer and the classification of an based on the ear.

+ Ts ₃ /an +	+ Ts ₃	++	an Ts ₃	an +
1941, tassels removed	174	109	5	288
1940, tassels not removed	183	80	8	238
+ Ts ₆ /an +	+ Ts ₆	++	an Ts ₆	an +
1941, tassels removed	75	36	17	67
1940, tassels not removed	213	159	50	151

The results of both plantings are essentially alike. One may conclude that the unequal nature of the complementary crossover classes is not primarily due to inaccuracies of classification but rather to some other cause.

Using the totals of both seasons, the following ratios occur:

Ts₃ cultures

370 Ts₃ : 715 + D/PE = .9 for 1:2 ratio

546 + : 539 an D/PE = .4 for 1:1 ratio

Ts₆ cultures

355 Ts₆ : 413 + D/PE = 3.1 for 1:1 ratio

483 + : 285 an D/PE = 3.3 for 2:1 ratio

In the Ts₃ data, Ts₃ is deficient while an is normal; whereas, in the Ts₆ data, Ts₆ is only slightly deficient and an greatly so. If these effects are due to an interaction between an and either Ts₃ or Ts₆ as Emerson 1941 News Letter (p. 15) suggests, the interaction is presumably different for the two tassel-seed genes.

M. J. Murray

3. Chromosome 7 linkage data - Professor A. C. Fraser made the following field plantings last spring and marked the seed-

lings. I assume all responsibility for the records on the mature plants and the following summary of the results (table 1).

Table 1. + + +/in v5 gl

<u>0</u>		<u>1</u>		<u>2</u>		<u>1-2</u>		<u>Total</u>
552	438	1	11	18	20	2	12	
990		12		38		14		1054

Recombination percentages: in-v5 2.4, v5-gl 4.8

Ratios: 573+ : 481 in, 593+ : 461 v5, 585+ : 469 gl

Percent non-germination of in seeds 20.6, of in seeds 28.4.

Fraser in News Letter 1938 (p. 11) reported in-v5 = 4.3% v5-gl = 12.2% where n = 1017 and in News Letter 1940 (p. 14) in-v5 = 6.% v5-gl = 14% where n = 10,563. The present records are obviously different from the previous ones in that crossing over in the v5-gl region is markedly reduced. While all the recessives were somewhat deficient, this in itself probably does not account for the reduced crossing over. Fraser (News Letter 1940) indicated that he was investigating the reason for marked differences in the complementary crossover classes in the in-v5 region. A study of the lineage of all these cultures may perhaps clarify the present results.

Table 2. + + +/v5 ra gl

<u>0</u>		<u>1</u>		<u>2</u>		<u>1-2</u>		<u>Total</u>
832	478	40	39	8	314	29	0	
1310		79		322		29		1740

Recombination percentages: v5-ra 6.2, ra-gl 20.2

Ratios: 909+ : 831 v5, 879+ : 861 ra, 1214+ : 526 gl

Fraser (News Letter 1941 p. 19) reported crossover percentages as follows: v5-ra 7, ra-gl 6, gl-ij 18. The present records agree for the first region but not for the second. However, the ratio of glossies to non-glossies is roughly 1:2.

Table 3. + + +/ra gl ij

<u>0</u>		<u>1</u>		<u>2</u>		<u>1-2</u>		<u>Total</u>
340	184	16	47	101	63	3	94	
524		63		164		97		848

Recombination percentages: ra-gl 18.9, gl-ij 30.8,

Ratios: 460+ : 388 ra, 582+ : 266 gl, 453+ : 395 ij.

The region ra-gl was also studied in another culture where 20.2 percent of crossing over was obtained. These two sets of data agree in fixing the length of this region at about 18-20 units. However, this is in contrast to the result of 6 units obtained by Fraser (News Letter 1941). The region gl-ii is longer (30.8) than in the previously reported data 18 (Fraser News Letter p. 19)

No final interpretation of these data will be attempted until I have had an opportunity to study the origin of all cultures. Even then, further work will probably be necessary.

M. J. Murray

4. Trisomics - Seed weight. In order to get a relatively high frequency of trisomic plants the smaller seeds are often selected from a trisomic ear. A study was made to find how close a correlation exists between weight of seed and chromosome number and whether this correlation varies in different trisomic stocks.

Random samples of from 50 to 150 seeds were taken from trisomic ears. In some cases, however, only relatively small numbers of seeds were available. Each seed was weighed to the nearest .01 gram and placed in its weight class. In most cases the weights when plotted against number formed a unimodal curve. In some, however, bimodal curves resulted (see III x lg2). The seeds were germinated in trays and roots taken before transplanting to the field. The results are expressed in table 1.

Table 1

Relative length of extra chromosome	Trisomic Stock	Weight of seed in mg.	% tri-somics	No. of individuals	% tri-somics in random sample	No. of individuals
85	II x L.F. Inbred	140-210	82	38	50	139
		220-230	53	59		
		240-260	19	42		
	II x Inbred II	160-220	14	7	37	43
		230-240	56	16		
		250-280	30	20		
	II x C. II Inbred	130-200	87	30	52	93
		210-230	49	35		
		230-260	18	28		
	II x lg	130-180	80	5	39	52
		190-200	61	18		
		210-240	17	29		
79	III x L.F. Inbred	150-240	69	16	35	34
		250-300	6	18		
	III x Inbred II	100-150	50	12	33	52
		160-180	40	20		
		190-230	15	20		
	III x lg 2	140-160	100	31	45	91
		170-180	50	16		
		190-240	5	44		
78	V x Inbred II	120-160	65	52	52	89
		170-230	32	37		
60	VI x su2	140-200	77	30	30	103
		210-220	12	42		
		230-260	10	31		
60	VII x L.F. Inbred	70-110	73	11	45	22
		120-150	18	11		
	VII x Inbred II	70-120	63	16	40	58
		130-140	39	23		
		150-200	21	19		

Relative length of extra chromosome	Trisomic Stock	Weight of seed in mg.	% tri- somics	No. of indi- vid- uals	% tri- somics in random sample	No. of indi- vid- uals
60	VIII x L.F. Inbred	110-170	63	38	32	146
		170-180	44	43		
		190-220	6	65		
	VIII x j	200-230	33	18	27	45
		240-260	33	18		
		270-320	0	9		
52	IX x v wx	120-160	46	13	22	113
		170-180	71	24		
		190-220	3	76		
45	X x L.F. Inbred	220-250	48	54	26	149
		260-270	12	52		
		280-310	12	43		
	X x <u>v</u> 18	200-230	58	12	37	49
		240-250	35	20		
		260-270	24	17		

Table 2

Relative length of extra chromosome	Trisomic stock	Percent		Percent	
		2n + 1 plants in pro- geny	No. of indi- viduals	microspores with n + 1 chromosomes	No. of indi- viduals
85	II. x L.F.	50	139	50	212
79	III. x lg2	45	91	41	167
45	X x L.F.	26	149	34	190
	X x <u>v</u> 18	37	49	33	109

Relative length of extra chromosome	Trisomic stock	Percent		No. of individuals
		microsporocytes with univalents in Met. I		
85	II. x L.F.	30		247
79	III. x lg2	-		-
45	X x L.F.	49		372
	X x <u>v</u> 18	37		300

5. Frequency of transmission of the extra chromosome in trisomes. Different trisomic stocks derived as maternal 21 chromosome plants from tetraploids show decided differences in percentage of trisomic plants in the progenies. Marked differences have also been observed in univalent frequencies, frequency of lagging in anaphase I and II and in other details of meiosis. A stock in which 40% of the progeny was found to be trisomic had one of the longer chromosomes in triplicate. Another stock producing 24% trisomic progeny had one of the shorter chromosomes in triplicate.

In order to test whether length of the extra chromosome can be correlated with frequency of transmission, known stocks have been studied. The data presented are incomplete but may be of some interest.

As the table indicates, the frequency of transmission of the extra chromosome through the egg varies from 22% to 52%. Different stocks of the same trisome show considerable variability in frequency of $2n + 1$ progeny. However, there is a strong positive correlation between length of the extra chromosome and the frequency with which it is transmitted through the egg. Several of the cases which are out of line may be due to the small number of seeds available.

Such explanations as abortion of ovules or differential seed viability would not seem to account for the observed differences in frequency of transmission since a close correspondence is found between the percentage of progeny which is $2n+1$ and the percentage of microspores with the $n+1$ number (see table 2).

Sporocyte studies, which have not yet been completed, indicate a greater frequency of univalents in the shorter chromosome stocks with more lagging in Met. I. and the formation of a greater number of micronuclei.

John Einset

Harvard University, Cambridge, Massachusetts

The readers of this News Letter may be interested in some of my observations on maize in Mexico. I spent the months of July and August in that country, travelled approximately 8,000 miles in fifteen states and visited a number of the experiment stations.

Maize is the universal crop in Mexico. It is grown from sea level to altitudes of approximately 10,000 feet. One sees it everywhere, planted between peach and apple trees in temperate regions; between bananas and pineapples in the tropics. It is frequently encountered as an ornamental plant in front yards and parks. Volunteer maize plants appearing in a garden or field devoted to other crops are usually allowed to remain.

The average Mexican apparently has the same feeling toward the maize plant which the Southern negro exhibits toward a water-melon vine. It distresses him to see it destroyed.

The diversity of maize in Mexico is enormous. Near El Seco we saw many fields in which the plants were tasseling out at a height of about two feet. Near Monterey we saw fields irrigated with sewage water with stalks fifteen feet in height. We did not see the famous giant corn of the Jala Valley except in experimental plantings at the station near Leon.

Much of the diversity, however, is environmental. In many respects Mexican maize is quite uniform. Practically all of the maize plants of the great central plateau of Mexico are highly pubescent and uniformly pigmented, either sun red or purple. Practically all of the maize in all parts of Mexico shows strong external indications of contamination with *Tripsacum*.

It is a common opinion in Mexico that maize reverts easily to teosinte. A very intelligent Canadian manager of a large estate assured us that teosinte-like segregates appear in the maize fields even when there is no teosinte in the vicinity to cause contamination. He is of the opinion that the potentialities for producing teosinte by recombination exist in many Mexican varieties.

A well-planned program of maize-breeding under the direction of Ing. Edmundo Taboado, Dirección de Agricultura, Mexico, D.F., is in progress at several stations. Ing. Eduardo Limon in charge of the Campo Experimental at Leon, Guanajuato, is one of the most enthusiastic of maize breeders.

Because of the Mexican trip, I missed for the first time in twenty years, the usual summer pollinating season. However the work carried on by J. W. Cameron during my absence has resulted in several interesting developments. The most important of these is a study of knob numbers on the chromosomes of Guatemalan varieties. Two hundred varieties were grown and knob numbers determined for 162 of these. The number varies from 1 to 16, and involves every previously encountered knob position in maize as well as two unusual positions on No. 10. Knob number is correlated with several other factors. Pubescent varieties had an average of 6.2 knobs as compared to 11.6 for non-pubescent types. Varieties with low knob numbers usually have tender brittle stalks which lodge easily; those with high numbers usually possess strong tough stalks. There is a relation between the altitude at which the corn was collected and knob number. Tentative averages based on the altitude data so far available are as follows:

500 meters	12.6 knobs
1000 "	10.7 "
1500 "	10.8 "
2000 "	7.5 "
2500 "	5.5 "

Finally, types described on the basis of the general appearance of the ear as "Andean" proved to have a low number of knobs, 4.7, as compared to the population as a whole, 7.9. The results are in general agreement with the hypothesis (Mangelsdorf and Reeves) that corn with knobless chromosomes was introduced from South America into Central America where it hybridized with *Tripsacum* to produce teosinte and new *Tripsacum*-contaminated varieties of maize with knobby chromosomes. The South American types apparently still persist in a relative state of purity at the higher altitudes in Guatemala.

P. C. Mangelsdorf

University of Illinois, Urbana, Illinois

1. The gene rt appears to be close to d (chromosome 3). In a progeny of eight plants (backcross repulsion phase), all the normal plants were rt and dwarf plants Rt.

2. The dwarf types reported in the 1941 News Letter may be located in chromosome 3, at about 24 (assuming the chromosome reversed with cr at 0).

3. A leaf spotting has been discovered in one of our inbred lines. It is a simple recessive to the normal.

C. M. Woodworth

University of Minnesota, University Farm, St. Paul, Minnesota

1. A new sugary, located by Horovitz in chromosome 6, was sent to me. A test with su2 indicates these two genes are probably alleles, although the test was not very clearcut.

2. Glossies - The third-leaf glossy, gl4 according to tests at that time, reported by Hayes as being linked with waxy (8% recombination, Coöp Letter April 1939), is the same as the Coöp, glossy 10, Coöp number C37-110 (1) (x). This glossy 10 is different from Sprague's glossy 10.

3. A group of unlinked genes is being tested for linkage in chromosome 6.

C. R. Burnham

4. Further studies have been made with chromosomal interchanges and the Minn. #13 smut resistant inbred line first reported by Saboe and Hayes, Jour. Amer. Soc. Agron. 33: 463-470. The long arms of #3, #7, and #8 and the short arm of #6 seem definitely to carry factors for smut reaction.

Lewis C. Saboe

Missouri Botanical Garden, St. Louis, Missouri

1. *Tripsacum*. With Dr. Hugh Cutler a preliminary survey of the genus *Tripsacum* has been published (separates available on request). The most important new fact turned up is a *Tripsacum* indigenous to South America from the Amazon Basin to Colombia. The numerous specimens from that region have at least one unique character and cannot therefore be recent introductions as had previously been supposed. The genus is so complex that it will take a decade to work out a complete and detailed monograph. In the meantime we shall be grateful for viable seeds or for chromosome counts of any species of *Tripsacum* from known localities.

2. Races of Maize. Cutler's collections of Mexican and Guatemalan maize have made it possible to begin another long-time project, the determination and description of the races of maize. While Sturtevant's classification (dents, flints, pops, etc.) is adequate as a cataloguing device there is also need for at least a rough grouping indicating general relationships in somewhat the same way that anthropologists analyze human variation. For such a grouping it is necessary to know as much as possible about the entire plant; tassel and leaf as well as ear and grain. We have therefore built up an herbarium of as many corn varieties as possible, including with the ear, herbarium specimens of seedlings, leaves, and tassels and notes on the number of nodes above the ear, the height of the plant, etc. For a considerable number of our collections duplicate specimens have been prepared in St. Louis, Texas, and Cuba. In addition to Cutler's collections we grew George Carter's extensive collection of Indian varieties from the southwest and a few unusual varieties such as Louisiana Gourdseed.

From an examination of the herbarium material the following characters were chosen as most indicative of general relationship: row number; kernel width, length, and thickness; mid cob width; number of tassel branches; length of glume (tassel); percentage of condensed internodes in tassel; pedicel length of pedicillate spikelet; percentage of sub-sessile pedicillate spikelets; length of sterile zone at base of tassel branches; pubescence of sheath.

By the use of these criteria our Mexican and Guatemalan collections can be divided into at least three main races, Big Grains, Mexican Pyramidals, and small-seeded Tropical Flints. The Big Grains are big cobbled and big kerneled with more or less enlarged butts. While they may be flour or flint they are characteristically more or less dented. The small-seeded Tropical Flints are not only exceedingly straight-rowed but the kernels are very uniform in diameter so that a row of them looks like a stack of pearl buttons seen from the side. They are all flints, have small cylindrical ears, and are prevailingly bright-colored. The Mexican Pyramidals are the common race in Mexico City and adjacent portions of the plateau. Important to U.S. corn breeding because most of their distinguish-

ing features, in a more or less diluted form, are found in cornbelt dents. They have a short pyramidal ear with long (often pointed) kernels. They are nearly all dents or semi-dents and the majority of them are white. They have few tassel branches and large glumes so that they are strikingly different from most other races and have been commented upon by Bonafous and Bukasov. The Indian corns of the southwest go into two races, the Pima-Papago and the Pueblo, the latter being closely allied to the Big Grains. Median values for representatives of these five races (and subraces) in our collections are as follows:

	Guatemala Big Grain	Tropical Flints	Pueblo	Pima- Papago	Mexican Pyramidal
Mid-cob width	30	22	26	22	20
Kernel width	10	7	9	8	8
Kernel thickness	5	3	5	5	4
Kernel length	10	9	10	8	14
No. of tassel branches	20	21	18	10	4
Length of sterile zone	8	7	8	5	3
Percent condensed internodes	0	0	10	0	40
Percent sub-sessile spikelets	0	0	0	10	50

It will be seen that on the whole the Big Grains are at one extreme and the Mexican Pyramidals are at the other. It is also to be noted that the Pima-Papago race while similar to the Tropical Flints in cob-size and grain-size is far removed from them in all other characters. Collins (in Guernsey and Kidder 1921) was therefore in error in identifying the prehistoric Basketmaker corn (which is practically identical with the modern Pima-Papago) with the Tropical Flints.

3. Southwestern races of maize. In the southwestern United States our collection of varieties is complete enough and the situation is so comparatively simple that we can generalize more completely than in Central America. Southwestern maize goes in two races plus a few obvious recent admixtures and an extensive series of intermediates between the two extremes. One race (the Pima-Papago) has been in the country a much longer time and is not now commonly grown by the Pueblo-dwelling Indians.

The Pueblo race is the big-shanked, long-eared, usually bright colored maize which is commonly sold to tourists. While it may be either flour or flint it has a strong tendency to be at least slightly dented. Characteristically it has short internodes immediately above the node of the upper ear and its tillers are morphologically unlike stalk in height, tassel, and ear. It is grown by all the Pueblo-dwelling Indians as well as

by the Navahos and Apaches.

The Pima-Papago corn, though extensively grown, is from districts so remote that it is seldom seen in collections. It is small-grained and small-cobbed and either white or bright light yellow. It is small-shanked and ears often taper as much to the butt as to the tip. While the kernels are in rows, the sulci between them are scarcely apparent and the kernels have somewhat the appearance of tiles in a mosaic. Characteristically the internodes of the main stem do not shorten above the ear and the tillers, in height, ear, and tassel are similar to the main stalk. It is grown by the Pima and the closely allied Papago and to a lesser extent by neighboring tribes. It is of peculiar interest because its ears are almost identical with those of the prehistoric Basketmaker Corn which according to dendrochronological reckoning appeared in the southwest about A.D. 300.

Since everyone to whom we have shown the collection has asked whether our work gives evidence for or against Mangelsdorf and Reeve's theory, it may be well to add that while in general it supports them, we have as yet no conclusive evidence for or against. It is already abundantly clear, however, that maize has had a complicated career in Central America.

We will be grateful for viable seed of old or unusual varieties.

Edgar Anderson

University of Missouri, Columbia, Missouri

1. Comparison of Xray and Ultra-violet Mutations of A. The origin of the Xray and UV mutants compared in this study, and observation on their phenotypic effects, viability and reaction to Dt, were given in the last News Letter. All three Xray mutants showed more or less reduction in gametophytic viability and were zygotically lethal; all four UV mutants were fully viable, regularly transmitted through male and female germ cells, and readily established as homozygous recessives.

This suggests that the Xray mutants are probably deficiencies too small for cytological identification and too slight in effect to be lethal in haplophase, but it leaves open the possibility that they are alleles of a with lowered viability.

With losses too small for cytological detection, the only proof of deficiency is genetic evidence of the loss of associated loci. McClintock's study of Bm ring-chromosomes showed the possibility of identifying loci in a deficiency through their effects upon tissue within a sector made homozygous deficient by loss or modification of the covering ring.

We were fortunately able to obtain a ring including the A

locus. The origin of this ring is an interesting story in itself, but it will not be included here. The ring carries the gene \underline{A}^b , and its behavior is similar to that described by McClintock. It is maintained in a stock otherwise homozygous for \underline{a} . Crossed on standard \underline{a} stocks it gives sectors of \underline{a} tissue in both the aleurone and the plant.

Ring bearing plants otherwise homozygous for the Xray mutant \underline{a}^{X4} were obtained for comparison by crossing and backcrossing as follows:

- (1) $\underline{a}^X \underline{a}^P \times \underline{a} \underline{a} \underline{A}^b$ -ring
- (2) $\underline{a}^X \underline{a}^P \times \underline{a}^X \underline{a} \underline{A}^b$ -ring
- (3) $\underline{a}^X \underline{a}^P \times \underline{a}^X \underline{a}^X \underline{A}^b$ -ring

Cross (1) gives mostly pale and colorless seeds, but also a considerable number of colored seeds, all of which are mosaic for pale or colorless. These are the ring-bearing individuals. Cross (2) yields mosaic colored seeds similarly, but among them there is included a new class in which the mosaic regions are of shriveled, degenerate tissue. These are the $\underline{a}^X \underline{a}^X \underline{A}^b$ -ring individuals. In cross (3) this class comprises nearly half of the mosaic seeds. The remainder (without degenerate tissue) are all phenotypically \underline{a}^P in the mosaic regions, and represent the $\underline{a}^X \underline{a}^P \underline{A}^b$ -ring class.

The sectors produced in plants grown from these two types of seed are very different. In the plants with \underline{a}^P the sectors are of wholly normal tissue, lacking only the anthocyanin characteristic of \underline{A}^b . They include both large and small sectors. In the plants homozygous for \underline{a}^X the sectors are small, and many show reduced growth leading to distorted development of the plant. Their most conspicuous feature is lack of chlorophyll. These sectors, whenever they occur in regions in which anthocyanin develops, show normal anthocyanin. In other words, they do not show the loss of \underline{A}^b . Very rarely a sector is found with loss of anthocyanin and with no loss of chlorophyll. In four cases we have found narrow sectors showing loss of both anthocyanin and chlorophyll, and each of these occurred as a secondary sector within a larger sector showing loss of chlorophyll without loss of anthocyanin.

We interpret this to mean that the mutant \underline{a}^{X4} represents the loss of not only the \underline{A} factor but also of a separable factor essential to chlorophyll development, and possibly of another essential to tissue survival. If the sectors showing loss of chlorophyll without loss of anthocyanin have the genetic constitution indicated by their phenotype, the separable viability factor must be assumed. The absence of primary sectors showing loss of both chlorophyll and anthocyanin would indicate that simultaneous loss of the two factors is lethal, while the occurrence of sectors deficient for both as a result

of consecutive losses would show that the lethal effect is not due merely to deficiency of these two factors. It would therefore have to be ascribed to a separable portion of the ring which is regularly eliminated when A and the chlorophyll factors are lost simultaneously. It is possible however that the sectors are in fact deficient for A^b. Their anthocyanin pigmentation is normal, but since the sectors are small it is possible that this may be a result of diffusion from the neighboring non-deficient tissue. If this is true, the assumption of a viability factor separable from A and the chlorophyll factor is not required.

The description given above for a^{X4} a^{X4}-Ring plants applies also to the compounds a^{X4} a^{X1}-Ring and a^{X4} a^{X6}-Ring. This shows that a^{X1} and a^{X6} also lack the associated factor or factors. We have not yet succeeded in producing a plant which could be proven to be homozygous a^{X1} a^{X1} A^b-ring or a^{X6} a^{X6} A^b-ring. It is possible that both a^{X1} and a^{X6} involve more loss than a^{X4}. a^{X6} is distinctly lower in male transmission than a^{X4}, while a^{X1} is distinct from both in having visibly defective pollen and no male transmission. The most extreme mutant, a^{X1}, reduces crossing-over between A and Et, though there is no visible indication of deficiency in the pachytene chromosome.

The results indicate that the apparent mutations of A induced by X-ray treatment are in fact minute deficiencies. The original series of X-ray-induced A-losses from which the mutants were selected included, in addition to obvious extreme deficiencies, several less defective plants with segregating pollen not wholly aborted but distinctly sub-normal in development. a^{X1} was a representative of this class. The A-losses with normally developed and partially functional pollen, a^{X4} and a^{X6}, apparently represent simply the extreme of the continuous series of intercalary deficiencies of varying length induced by X-ray treatment.

On the contrary, the UV mutants, a^{U3}, a^{U15}, and a^{U18}, similarly tested with the ring-chromosome, behave precisely as do the standard alleles, a^P and a, and their sectors are phenotypically identical with those of standard a.

The UV mutants, unlike the X-ray mutants, appear in the F₁ from treated pollen as a class distinct from the deficiencies produced by the treatment. The series of UV-induced A-losses included, in addition to the three mutant a's and the intermediate allele A^{lt}, a large number of extreme deficiencies with distinctly defective growth and aborted pollen, but none of the intermediate type with subnormal pollen. This may be due to the rarity of intercalary deficiencies induced by this agent. Although it is reasonable to assume that intercalary deficiencies may sometimes be induced by UV (since translocations are), it is clear that the UV mutations are much too frequent to be accounted for in the way suggested above for the X-ray mutations.

If the UV mutants are deficiencies they are deficiencies of a different order. They show no difference from standard a except in their failure to mutate under the influence of Dt. As previously stated (News Letter 1941: 45), this is not convincing evidence against intragenic mutation.

L. J. Stadler and Herschel Roman

2. Translocations involving B chromosomes. Eight translocations between A and B chromosomes have been obtained from B-bearing pollen treated with Xrays. The A chromosome of six of these has been identified and the approximate position of breakage points determined, as follows:

Translocation	Cytological Position	
	A chromosome	B chromosome
T1-B	S .1	heterochromatin
T2-B	S .2-.3	junction*
T4-B	S .2	junction
T6-B	S (dividing nucleolar organizing body)	heterochromatin?
T7a-B	L .9-1.0	junction
T7b-B	L .35	euchromatin

*This is the junction of the euchromatic region and the large heterochromatic region.

All of these except T7a-B were tested for male and female transmission. The female transmission was quite normal but the male transmission was distinctly low. For example, a plant heterozygous for T2-B in which the translocation was marked by V4 and the normal chromosome by v4, when used as the male parent on homozygous v4, gave 80 V4 : 164 v4 F_1 seedlings. There is considerable crossing over between V4 and the point of breakage so that the frequency with which the translocation is transmitted is less than the ratio indicates. Similar crosses with T4-B, in which the translocation was marked by Su and the normal chromosome 4 by su, when crossed on su gave 253 Su : 797 su. Since very little, if any, crossing over occurs between Su and the point of breakage the ratio of Su : su probably represents a close approximation of the frequency with which T4-B is transmitted.

Evidence that a heterozygous A-B translocation when used as the male parent produces hypo- and hyperploid F_1 plants suggested that the low male transmission was a result of non-disjunction in the second microspore division. Hyperploid plants from T1-B, T2-B, T4-B, T7a-B, and T7b-B were identified cytologically and were found to contain the heterozygous translocation plus an extra translocation chromosome. Thus the extra chromosome must have resulted from non-disjunction either at meiosis or elsewhere. In every case the extra chromosome

was the translocation chromosome which possessed the B chromosome centromere.

The production of hypoploids was demonstrated when plants heterozygous for an A-B translocation and carrying only dominant factors were crossed on plants carrying appropriate recessives. The data from this type of cross are given in the following table.

<u>Crosses</u>	<u>Frequency of recessives appearing in F₁</u>	<u>Per Cent</u>
<u>Su su</u> x T4-B/normal, <u>Su Su</u>	52 <u>su</u> /423	25*
<u>su</u> x T4-B/normal, <u>Su Su</u>	31 <u>su</u> /92	34
<u>O2 gl</u> x T7b-B/normal, <u>O2 O2 Gl Gl</u>	0 <u>o2</u> /63	0
	21 <u>gl</u> /63	33
<u>Ij ij Gl gl</u> x T7b-B/normal, <u>Ij Ij Gl Gl</u>	6 <u>ij gl</u> /42	28*

*These values have been corrected for the fact that the female parent was heterozygous rather than homozygous recessive.

The appearance of the recessive character in the F₁ is due to the loss of the translocation chromosome bearing the factor for the corresponding dominant. Since Gl is nearer the end of the long arm of chromosome 7 than O2, the loss of Gl without the loss of O2 must mean that the absent chromosome is the one possessing the B chromosome centromere.

Proof that non-disjunction occurs at the second microspore division was obtained from a cross using a hyperploid plant from T2-B as the male parent. Twenty-three F₁ plants were examined cytologically. Of the twenty-three, twelve were hyperloid like the male parent; seven were euploid, heterozygous for the translocation; and four were euploid, homozygous normal. The occurrence of twelve hyperploid plants, which could have resulted only from non-disjunction, and the absence of other classes that would be expected with the same frequency from non-disjunction elsewhere show that non-disjunction occurs only at the second microspore division.

The frequency with which non-disjunction occurs may be roughly estimated from the data in the table demonstrating hypoploidy. The maximum frequency with which the recessive may appear is 25% (corresponding to 100% non-disjunction) if the hypoploid plants are viable (as they certainly are in the case of T7b-B and probably also in T4-B). The fact that the observed frequencies equal and exceed this value cannot be taken too seriously since these data were obtained from a limited series of crosses and may be effected by the presence of associated transmission factors. It is known from cytological

evidence that the frequency of non-disjunction is not 100%. But the data do suggest a very high frequency and further experiments to determine this with accuracy in each of the A-B translocations are in progress.

Will non-disjunction account for the anomalous male transmission of the intact B chromosome? The combined data of Longley and Randolph, from a cross of a 1B male on a 0B female, gave 108 plants with no B chromosomes, 35 with 1, 20 with 2, and 2 with 3 B chromosomes. We should expect, from 50% non-disjunction, 103 plants with no B's, 41 with 1, 21 with 2, and none with 3 B chromosomes. The observed 3 B chromosome plants may be accounted for in other ways. The close fit indicates that the mechanism for the aberrant male transmission of A-B translocations is identical with that of the intact B chromosome.

Can we localize the cause of non-disjunction within the B chromosome? The heterochromatic region may be excluded as a factor in non-disjunction for in T7b-B the chromosome undergoing non-disjunction does not contain this region. Furthermore, non-disjunction is not related merely to the shortness of the chromosome for in the case of T1-B the translocation chromosome undergoing non-disjunction is longer than the normally behaving short A chromosomes. Consequently, the cause of non-disjunction is related to the position or the special nature of the B chromosome centromere or to some factor in the proximal portion of the euchromatic region of the chromosome.

3. Some uses of A-B translocations. The B chromosome provides a centromere to which specific segments of A chromatin may be translocated. The exceptional behavior of the resultant chromosome in the second microspore division provides a mechanism for the accumulation of this chromosome for various cytogenetic problems in which duplications are useful. One application of this, now in progress, is a study of the effect of accumulation on the phenotype of recessive and intermediate alleles, using T2-B for a comparison of B, B^W, and b in various doses.

The fact that A-B translocations produce functional gametes deficient for as much as a whole arm of an A chromosome provides a tool for the location of recessive genes in the physical chromosome in a single generation. One would simply cross known A-B translocations on the recessive in question. If the locus of this gene is in the translocation chromosome with the B centromere, the recessive phenotype will appear in the F₁. For example, if the recessive is located in the distal four-fifths of the short arm of chromosome 4, it will appear in the F₁ of a cross by T⁴-B. The results summarized in the table place Su in this region. Likewise G1 and Ij are in the distal two-thirds of the long arm of chromosome 7, whereas O2 is not in this segment. An extensive planting for new A-B translocations involving different segments of the A chromosomes is planned for this summer.

Herschel Roman

4. The Anthocyanin Pigments of Corn. According to Sando et al, the plant pigment of purple corn (A B Pl R^r) is chrysanthemin. The anthocyanin pigments present in other types have not previously been reported.

The anthocyanins which occur most commonly as flower color pigments (glycosides of pelargonidin, cyanidin, delphinidin, peonidin, malvidin and petunidin) may be identified by simple qualitative tests outlined by Robinson and Robinson. The reactions of many less commonly occurring anthocyanins and of some synthetic anthocyanins not known to occur naturally have been summarized by Karrer.

Robinson's qualitative tests have been applied to the pigments extracted from numerous genetic types of corn. Although some of the pigments were identifiable with the qualitative tests, there were several which proved to be distinctly different in their reactions from the common flower pigments listed above.

An F₂ of the hybrid a pr b pl R^G x A Pr B Pl R^r was closely examined for color variations. In addition to the familiar plant color types expected from this cross, there were various minor modifications which have not previously been analyzed genetically. Plant material was taken from many of these plants for analysis, and all of the plants were self-fertilized.

The "A" type plants (A B Pl) in this hybrid population fall into three fairly distinct groups: (1) deep bluish purple, (2) deep reddish purple (maroon) and (3) light, distinctly reddish purple (dilute). The anthocyanins extracted from these plants included typical pelargonidin as well as typical chrysanthemin, and also in several cases pigments giving a typical reaction. The pigment differences are not always evident from the external appearance of the plant. Both chrysanthemin and pelargonidin are found among the deep bluish purple plants and among the maroon plants, but chrysanthemin is not found in the "dilute" class.

In F₃, pure breeding families of the above described types were established. One deep bluish-purple family contained typical chrysanthemin. One deep bluish purple, indistinguishable from the chrysanthemin family except by anther color, contained a pigment which differed only slightly in reactions from pelargonidin 3-monoside, and one family of reddish purple (maroon) had pigment apparently identical to that of the deep purple pelargonidin type. A pure breeding "dilute" family showed typical pelargonidin 3-monoside reactions.

The pigment of "B" type plants (A B pl) showed reactions not typical of any of the commonly occurring anthocyanin types. Although there was variation in intensity of pigmentation comparable to that among the "A" type plants, no differences in the pigment of the different "B" type plants have been established.

The variation in intensity of the "E" type (aBFl) plants is correlated, at least to a large extent, with that of "A" type plants. In families with "A" type plants mostly deep purple, the "E" types were mostly deep brown and in families of "dilute" pigmentation it was difficult to distinguish a B Pl from a B Pl plants until the plants were nearly mature.

The pure breeding pelargonidin families of this stock were recessive pr but in many plants of this hybrid the Pr separation was doubtful. Therefore tests were made on different hybrids with positive Pr separation to establish this relation. In the first planting, the Pr plants, (6 in number) all contained chrysanthemin and the pr plants (8 in number) pelargonidin 3-monoside. In tests on the Pr and pr plants from six ears of the progeny of this family (self-fertilized or back-crossed) the same results were obtained. The pigment was found to be the same in all parts of the plant, including roots, coleoptile, sheath, husks, cob and aleurone.

Analyses have been made of pigments characteristic of other A alleles, in plants with B and Pl. A^b gives chrysanthemin indistinguishable from that of A plants of the same culture. Standard aP, several mutant aP's (by spontaneous mutation from A^b), and A^{lt}, (an ultraviolet mutant of A), all give mixtures of anthocyanin and flavonol in varying proportions. The anthocyanin in these mixtures, however, is distinct from that produced by A and A^b, and resembles in some reactions the pigments of sun-red plants.

J. E. McClary

5. Experiments on Gene Action in Anthocyanin Synthesis. In those genotypes which normally produce anthocyanin in the root, excised roots cultured on media containing glucose and mineral nutrients produce anthocyanin abundantly. Anthocyanin therefore may be synthesized by the cell from externally supplied glucose, without the intercession of other substances derived from the overground parts of the plant. The genes essential for root color in the dark are A (or A^b), A₂, Pl, and a suitable R allele (R^{ch}, r^{ch}, and some but not all R^r's and r^r's). B is not essential and does not replace R^r.

It may be possible to learn something of the course of synthesis of anthocyanin, and of the role of various genes affecting it, by physiological experiments with excised tissues, testing the effects of postulated intermediates between glucose and anthocyanin, of specific enzyme inhibitors, of diffusible substances extracted from plants of contrasting genotype, etc.

Experiments with intermediates supplied in place of glucose cannot well be made with excised root-tip cultures, because the addition of some glucose or fructose is necessary to keep the roots growing. An intermediate would have to replace glucose in general metabolism as well as in anthocyanin

synthesis to give positive results. Minimal quantities of sugar will maintain slow growth with little or no anthocyanin production, and experiments may be made with intermediates added to increase the anthocyanin yield.

A more satisfactory technique is to use sections of mesocotyl or leaf blade from young seedlings, since cell division is not a factor and since differentiated cells capable of anthocyanin production are present from the start. These sections remain alive for several days in buffer solutions, dilute salt solutions, or pure water. In suitable genotypes, they fail to produce anthocyanin unless sugar is added, while with added glucose or fructose they produce anthocyanin abundantly. Although these sections may contain reserve carbohydrate which may be used in the synthesis of anthocyanin, they cannot complete the synthesis without something which they obtain from added glucose.

Leaf blades from mature plants also serve very well in r^{ch} stocks (with A b Pl), and quite well in R^{ch} . Anthocyanin is produced poorly in mature leaf tissues with the best of the R^r and r^r alleles tested, and not at all with some. Mature leaves are convenient material, especially for producing the quantities of pigment required for chemical analysis.

Several preliminary experiments of this type were performed this winter, and some of the results are summarized below.

Galactose, which does not support the growth of excised root tips, may be substituted for glucose in the production of anthocyanin in leaf or mesocotyl tissue. On the contrary, mannose, l-sorbose, and l-rhamnose give no anthocyanin.

The pentoses, xylose and lyxose, give a good yield of anthocyanin, while arabinose (both d- and l- forms) and ribose fail.

Some modifications of the C_1 and C_6 groups in the glucose molecule may be made without preventing the production of anthocyanin. Sorbitol and glucuronic acid yield anthocyanin; -methyl-glucoside and gluconic acid do not.

The trioses, glyceraldehyde and dihydroxyacetone, in phosphorylated form, are produced from glucose in the normal course of respiration. Either glyceraldehyde or dihydroxyacetone (unphosphorylated), supplied in place of glucose, will permit the production of some anthocyanin, more in the case of glyceraldehyde than of dihydroxyacetone.

Various specific enzyme inhibitors or poisons have been supplied over a range of concentration extending to the toxic limit, without producing a distinct reduction in the yield of anthocyanin from glucose. These include cyanide, azide, iodoacetate, fluoride, malonic acid, urethane and maleic acid. Certain other inhibitors show possible effects which are still

under study. The only substance which in catalytic concentrations shows inhibition of the production of anthocyanin from glucose, in the trials made so far, is 2-4-dinitrophenol. This is a well-known stimulant of respiration and glycolysis, and may reduce anthocyanin synthesis competitively by diverting glucose to other channels. At concentrations of the order of 10^{-5} molar it inhibits anthocyanin production, and at lower concentrations it reduces materially the quantity of anthocyanin produced.

A possible hypothesis is that anthocyanin is produced by condensation of two phenol derivatives, related to phloroglucinol and catechol, with a 3C unit derived from glyceraldehyde. The effect of A would be a reduction in the 3C unit, which might occur either before or after the condensation. If the reduced 3C substance in A stocks were glyceraldehyde itself, it might be possible to produce anthocyanin in tissue lacking the A gene by supplying this substance. This was tried, unsuccessfully, with a, a^D, A^{lt}, and a₂. Similar trials with dihydroxyacetone, glycerol, and hydroxypyruvic aldehyde (all of which produce some anthocyanin in A tissue) also failed. Experiments in this direction with various 3C substances are being continued, together with analogous experiments with catechol derivatives and 6C-3C compounds in relation to the Pr effect.

The experiments mentioned are of course merely exploratory trials, made chiefly to test the feasibility of the general approach and to determine which aspects, if any, have sufficient promise to justify more intensive study. Obviously, neither the positive nor the negative effects of specific substances upon anthocyanin production may be interpreted in terms of the place of these substances in biosynthesis, without careful study of their other physiological effects.

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* Backcross data indicating the order of the genes gs2, B and lg are given below.

		<u>0</u>	<u>1</u>	<u>2</u>	<u>1-2</u>
<u>+</u>	<u>B</u>	107	104	46	38
<u>gs2</u>	<u>lg</u>	211	11	84	4
<u>+</u>	<u>+</u>				
					310

The linear order and map distances are: gs2 4.8 B 28.4 lg.

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Below are given the results of a backcross test with Golden 2 against translocation 3-7b. In the light of our earlier report (M.G.C. N.L., 3-23-37, p. 14) that g2 was possibly linked with d, the indication is that g2 is in chromosome 3. Chromosome 7, however, is not excluded.

	T+	Tg2	++	+g2	
<u>g2</u> T3-7b	139	19	19	160	= 337

Percent recombination = 11.3

R. A. Brink and D. C. Arny

III. MAIZE PUBLICATIONS

There is presented here a list of papers on maize, probably an incomplete one. No long search of the literature has been made. Fraser did a better job last year.

R. A. Emerson

Abbe, Ernst C., L. F. Randolph, and John Einset - The developmental relationship between shoot apex and growth pattern of leaf blade in diploid maize. *Amer. Jour. Bot.* 28: 778-784. 1941.

_____ and B. O. Phinney - The action of the gene dwarf 1 in the outogeny of the stem of maize. *Abst. in Genetics* 27, p. 129. 1942.

Anderson, E. G. - Translocations in maize involving the short arm of chromosome 1. *Genetics* 26: 452-459. 1941.

Bair, R. A. and W. E. Loomis - The germination of maize pollen. *Science* 94: 168. 1941.

Blanchard, Ralph A., John H. Bigger and Ralph O. Snelling - Resistance of corn strains to the corn ear worm. *Jour. Amer. Soc. Agron.* 33: 344-350. 1941.

Burnham, C. R. - Cytogenetic studies of a case of pollen abortion in maize. *Genetics* 26: 460-468. 1941.

Clark, Frances J. - Preliminary investigations in Zea mays of the germination capacity of pollen with aberrant nuclei. *Abst. in Genetics* 27, p. 137. 1942.

Cunningham, J. C. - Maize bibliography for the years 1917 to 1936, inclusive. *Contributions. Iowa Corn Research Institute* 2: 1-364. 1941.

Cutler, Hugh C. and Edgar Anderson - A preliminary survey of the genus *Tripsacum*. *Ann. Mo. Bot. Gard.* 28: 249-269. 1941.

Jenkins, M. T. - The segregation of genes affecting yield of grain in maize. *Abst. in Proc. Seventh Intern. Gen. Cong.*, p. 168. 1941 (1939)

Jones, Donald F. - Somatic segregation. *Bot. Rev.* 7: 291-307. 1941.

_____ - Segmental exchange in somatic cells of maize. *Proc. Intern. Gen. Cong.* p. 170. 1941 (1939).

- Khankhoje, P. - Un nuevo e interesante hibrido de maiz tunicata (Zea mays tunicata) con polen de teocintle (Euchlaena mexicana Schrad.) Mem. Acad. Nacion. Cierc. "Antonio Alzate" 55: 83-94. 1940.
- Lindstrom, E. W. - Analysis of modern maize breeding principle and methods. Proc. Seventh Intern. Gen. Cong. pp. 191-196. 1941 (1939)
- _____ - Inheritance of seed longevity in maize inbreds and hybrids. Abst. in Genetics 27, p. 154. 1942.
- Longley, A. E. - Chromosome morphology in maize and its relatives. Bot. Rev. 7: 263-289. 1941.
- _____ - Knob positions on teosinte chromosomes. Jour. Agric. Res. 62: 401-413. 1941.
- Mangelsdorf, P. C. - The origin of maize. Abst. in Proc. Seventh Intern. Gen. Cong. p. 209. 1941 (1939).
- McClintock, Barbara - The association of mutants with homozygous deficiencies in Zea mays. Genetics 26: 542-571. 1941.
- Randolph, L. F. - An evaluation of induced polyploidy as a method of breeding crop plants. Amer. Nat. 75: 347-363. 1941. (Includes a discussion of polyploid maize and teosinte. Ed.)
- _____ - Genetic characteristics of the B chromosomes in maize. Genetics 26: 608-631. 1941.
- _____ - The influence of heterozygosis on fertility and vigor in autotetraploid maize. Abst. in Genetics 27, p. 163. 1942.
- Rhoades, M. M. - On the high mutation rate of the a allele in maize induced by the Dt gene. Proc. Seventh Internal. Gen. Cong. pp. 247, 248. 1941 (1939).
- _____ - Different rates of crossing over in male and female gametes of maize. Jour. Amer. Soc. Agron. 33: 603-615. 1941.
- Roberts, E. and Irwin R. Horner. Causes of preferences exhibited by animals for certain inbred strains of corn. Jour. Amer. Soc. Agron. 33: 448-453. 1941.
- Roberts, Lewis M. - The effects of translocations on growth in Zea mays. Abst. in Genetics 27, p. 166. 1942.
- Roman, Herschel - Translocations involving "B" chromosomes in maize. Abst. in Genetics 27, p. 167. 1942.

- Rosenquist, C. E. - The effect of tillers in corn upon the development of the main stalk. Jour. Amer. Soc. Agron. 33: 915-917. 1941.
- Saboe, Lewis C. and H. K. Hayes - Genetic studies of reactions to smut and to firing in maize by means of chromosomal translocations. Jour. Amer. Soc. Agron. 33: 463-470. 1941.
- Shafer, John, Jr. and R. G. Wiggans - Correlation of total dry matter with grain yield in maize. Jour. Amer. Soc. Agron. 33: 927-932. 1941.
- Singleton, W. R. - Hybrid vigor and its utilization in sweet corn breeding. Abst. in Proc. Seventh Intern. Gen. Cong. pp. 264, 265. 1941 (1939).
- _____ - Hybrid vigor and its utilization in sweet corn breeding. Amer. Nat. 75: 48-60. 1941.
- Sprague, G. F. and A. A. Bryan - The segregation of genes affecting yield prepotency, lodging, and disease resistance in F_3 and F_4 lines of corn. Jour. Amer. Soc. Agron. 33: 207-214. 1941.
- Stadler, L. J. and Fred M. Uber - Genetic effects of ultra-violet radiation in maize. IV. Comparison of monochromatic radiations. Genetics 27: 84-118. 1942.
- Tavcar, A. - Inheritance of 2-, 3-, 4- and 6-articulate leaf whorls in Zea mays L. Abst. in Proc. Seventh Intern. Gen. Cong. pp. 295, 296. 1941 (1939).

IV. Inventory of Seed Stocks Propagated in 1940 and 1941

A complete list of all Coop. stocks on hand at the close of the 1939 season appeared in the 1940 News Letter. The symbol (x) = selfed and # = sib crossed.

1940

- Co 40-1 and 2 (x) Inbred I (U.S. 204) P^{wr} Y A b pl, also pollinated with y Hadjinov's gl₅, may seg. v_x (98); may seg. pr yg_a (88); P^{wr} Y cr "white stripe", may seg. wx pg₂ lg_x (95); gl₄, may seg. y pr c sh wx ws (118); may seg. y wx B Pl f Hadjinov's gl₈ (101); seg. at, may seg. y I? sl ts₂ br f bv (107); pr v₃, may seg. su (61); lg B/A/Pr/ y pl/C R^{gg}/bm_x S_x, may seg. v_x (69); P^{wr}, may seg. y pr R^{gg} R^{nj}? su B Pl lg_x g d₇ v_x (115); su^{am}? ba₂, may seg. y pr Pl v_x f? lg_x (112); Y rt, may seg. pr Pl d_x bl? (124); P^{wr} Y f_x pk? sk_x, may seg. ms_x d_x (74); Y A b Pl vb, may seg. P v_x (109); P a sh wx f lg_x, may seg. su (71); ws₂?, may seg. y pr li g (119); sh pk, may seg. y lg_x v_x or l_x (64); may seg. pr su wx? pg_a (94); y a C r pr wx, may seg. ys_x (116); wx? may seg. y Bn? an_x v₆ d_x cr_x (81); P a br f, may seg. bm₂ nl₂ w_x (123); may seg. d_x^s d^D (114); A B pl Rg Lg₃ d^s, may seg. y Bn? an_x (129); 34 ears
- " 40-3 and 4 (x) Inbred II (West Branch) Y A b pl, also pollinated with P^{wr} Y cr "white stripe", may seg. wx pg₂ lg_x (95); lg B/A/Pr/y pl/C/R^{gg}/bm_x S_x, may seg. v_x (69); Y rt, may seg. pr Pl d_x bl? (124); may seg. pr su pg_a (94); Pr, may seg. P pg g (65); 14 ears.
- " 40-5 and 6 (x) Dutton's Flint Inbred Y, also pollinated with P^{wr}, may seg. y pr R^{gg} R^{nj}? su B Pl lg_x g d₇ v_x (115); Y rt also Rg, may seg. pr Pl d_x bl? (124); P^{wr} Y f_x pk? sk_x, may seg. ms_x d_x (74); Y cr_x, may seg. Bn? v₆ d_x (82); "Deep Y" lg gl₄, may seg. v_x bm_x (103); lg B/A/Pr/y pl/C/R^{gg}/bm_x S_x, may seg. v_x (69); seg. sk, may seg. P^{wr} y d_x bl_x v_x cr_x (84); sh pk, may seg. y lg_x v_x or l_x (64); f, may seg. y wx B Pl Hadjinov's gl₈ (101); Y wx?, may seg. pr su ar_a (93); 19 ears
- " 40-7 (x) F₂ involving P^{wr} Y Pr wx, may seg. yg_a; 3 ears
- " 40-8 (x) F₂ involving P sk, may seg. v_x lg_x; 4 ears
- " 40-9 (x) " " P^{wr} Y y Pr su sp?; 4 ears
- " 40-10 (x) F₂ " P^{wr} Y zb₄; 3 ears
- " 40-11 (x) " " P^{wr} Y R^{mb}, may seg. j; 1 ear
- " 40-12 (x) " " P^{wr} Y y Rst Pr; 1 ear
- " 40-13 (x) " " P^{wr} Y y A C R^{nj} Pr wx?; 5 ears
- " 40-14 (x) " " P^{wr} Y y R^{gg} Pr; 3 ears
- " 40-15 (x) " " P^{wr} P^{VV} Y y A C R^{gg} Pr su; 4 ears

Co 40-16	(x)	F ₂	involving	PWR Y v7-stripped; 3 ears
" 40-17	(x)	"	"	PWR Y o B v _x ; 5 ears
" 40-18	(x)	"	"	P Y a ^p B Pl, seg. b pl; 5 ears
" 40-19	(x)	"	"	PWR Y y wx? vl8; 4 ears
" 40-20	(x)	"	"	PWR Y fs; 5 ears
" 40-21	(x)	"	"	PWR Y y zb4 br f bm2 wx?; 3 ears
" 40-22	(x)	"	"	PWR Y A b lg gl2 ts v4, seg. Pl; 4 ears
" 40-23	(x)	"	"	PWR Y y A b pl ws3 lg gl2; 4 ears
" 40-24	(x)	"	"	PWR Y y A b pl lg gl2 fl v4; 5 ears
" 40-25	(x)	"	"	PWR Y y d lg2, seg. an _x , may seg. pm; 5 ears
" 40-26	(x)	"	"	PWR Y y d a lg2, may seg. ts4; 5 ears
" 40-27	(x)	"	"	PWR Y y sh wx gl4 v _x ; 3 ears
" 40-28	(x)	"	"	PWR Y yg2 sh wx gl4 lg; 5 ears
" 40-29	(x)	"	"	PWR Y y wx gl4 v _x ; 4 ears
" 40-30	(x)	"	"	PWR Y y zb5, may seg. g nl; 3 ears
" 40-31	(x)	"	"	PWR Y y Pl "brown stripe", may seg. msll ar-like stripe; 2 ears
" 40-32	(x)	"	"	Y Pr wx, may seg. yg _a ; 4 ears
" 40-33	(x)	"	"	P Y y sk, may seg. v _x lg _x ; 4 ears
" 40-34	(x)	"	"	Y y Rst? Pr su sp?; 3 ears
" 40-35	(x)	"	"	Y zb4; 5 ears
" 40-36	(x)	"	"	Y Rmb, may seg. j; 4 ears
" 40-37	(x)	"	"	Y y Rst Pr; 4 ears
" 40-38	(x)	"	"	Y y Rgg Pr; 4 ears
" 40-39	(x)	"	"	PVV Y A C Rrg Pr pr wx?; 5 ears
" 40-40	(x)	"	"	Y y Wh? su r ^{rr} ; 3 ears
" 40-41	(x)	"	"	PWR Y v7-stripped; 4 ears
" 40-42	(x)	"	"	Y o v _x ; 3 ears
" 40-43	(x)	"	"	P Y y a ^p B Pl, seg. b pl p; 4 ears
" 40-44	(x)	"	"	Y fs; 2 ears
" 40-45	(x)	"	"	Y y zb4 br f bm2 wx?; 4 ears
" 40-46	(x)	"	"	Y y y _x ? ws3 lg gl2; 5 ears
" 40-47	(x)	"	"	Y y lg gl2 fl v4; 4 ears
" 40-48	(x)	"	"	PWR Y d lg2, may seg. pm; few seeds
" 40-49	(x)	"	"	Y yg2 sh wx gl4 lg; 4 ears
" 40-50	(x)	"	"	Y y wx gl4 v _x ; 5 ears
" 40-51	(x)	"	"	Y y "brown stripe", seg. B Pl P, may seg. msll ar-like stripe; 4 ears
" 40-52	(x)	F ₃	"	Inbred I and PWR Y wx g4; also crossed with Y wx g4 (59); 11 ears
" 40-53	(x)	"	"	Inbred I and PWR Y y ra sl, also crossed with Y y ra sl (56); 14 ears
" 40-54	(x)	"	"	Inbred I and PWR Y bm3, also cross- ed with Y bm3 (57); 15 ears
" 40-55	(x)	"	"	Inbred I and PWR Y wx g4, also crossed with Y wx g4 (58) and Y wx g4 (59); 14 ears
" 40-56	(x)	and #F ₃	"	Inbred II and Y y ra sl; 13 ears
" 40-57	(x)	"	"	Inbred II and PWR Y bm3, also crossed with Y bm3 (54); 20 ears

- Co 40-58 (x) and #F₃ involving Inbred II and Y wx g⁴, also
crossed with Y wx g⁴ (52)
and Y wx g⁴ (55); 13 ears
- " 40-59 (x) F₃ involving Inbred II and Y wx g⁴, also crossed
with Y wx g⁴ (52); 12 ears
- " 40-60 (x) y, may seg. g³ l_x, (freezing injury, poor germ-
ination); 1 ear
- " 40-61 (x) pr v₃, seg. su, also pollinated with Inbred I
(1) and Inbred II (3) and recip-
rocally with Inbred I (1); 6 ears
- " 40-62 (x) P^{W^r} y, seg. ms¹⁸ bm lg_x, may seg. pg_x or l_x,
also pollinated with Inbred I
(1 and 2); 3 ears
- " 40-63 (x) and # gl, seg. Wh sl_x, also pollinated with In-
bred II (3); 4 ears
- " 40-64 (x) and # sh pk, seg. y lg_x, may seg. v_x or l_x, also
crossed onto Inbred I (1) and
Dutton's Flint Inbred (5); 3 ears
- " 40-65 (x) and # Pr g, seg. P pg, also pollinated with In-
bred II (3) and reciprocally with
Inbred II (4); 6 ears
- " 40-66 (x) y r g, may seg. pr su l₂, also pollinated with
Inbred I (1); 3 ears
- " 40-67 (x) Seg. Pr pr ms_x, may seg. pg? pb? zb? and usually
completely sterile plants with
necrotic leaves, also pollinated
with Inbred I (1), Inbred II (3)
and y +/po (121); 7 ears
- " 40-68 (x) Seg. y Rst Pr, may seg. l_x ms_x, also pollinated
with Inbred I (1 and 2) and Inbred
II (3); 10 ears
- " 40-69 (x) and # lg B/A/Pr/y pl/C/RGG/bm_x S_x, may seg. v_x,
also pollinated with Inbred I
(2) and reciprocally with Inbred
I (1), Inbred II (3) and Dutton's
Flint Inbred (5); 9 ears
- " 40-70 (x) and # y a C R pr in j lg, also pollinated with
Inbred I (1); 8 ears
- " 40-71 (x) and # P a sh wx f, seg. su lg_x, also pollinated
with Inbred I (1) and Inbred II
(3) and reciprocally with Inbred
I (1 and 2); 10 ears
- " 40-72 (x) P a sh wx su lg f (freezing injury, poor germina-
tion); 4 ears
- " 40-73 (x) and # a B Pl lg v₄, seg. y ts; 7 ears
- " 40-74 (x) P^{W^r} Y pk?, seg. sk_x, ms_x, may seg. d_x f_x, also
pollinated with Inbred I (2) and
reciprocally with Inbred I (1)
and Dutton's Flint Inbred (5);
3 ears
- " 40-75 (x) su, seg. y sh, may seg. vl₄ d₃ w_x; 2 ears
- " 40-76 (x) and # P A B pl sh, seg. cr_x wx?, may seg. l₆;
3 ears

- Co 40-77 (x) and # Pr, seg. sh Ts_x, may seg. v8 d_x, also pollinated with Inbred I (1 and 2), (freezing injury, poor germination); 10 ears
- " 40-78 (x) and # Y, seg. su fl_x v_x cr_x, may seg. d_x v8, also pollinated with Inbred I (1) and Inbred II (3); 12 ears
- " 40-79 (x) y su, seg. f_x, may seg. d_x v8, also pollinated with Inbred I (2), (freezing injury, poor germination); 2 ears
- " 40-80 (x) Y, seg. su fl_x v_x, may seg. v8 d_x, also pollinated with Inbred I (2) and Inbred II (3); 8 ears
- " 40-81 (x) wx?, seg. PWR y Bn? d_x an_x, may seg. v6 cr_x, also pollinated with Inbred I (2) and reciprocally with Inbred I (2); 10 ears
- " 40-82 (x) and # Y cr_x, seg. Bn?, may seg. d_x v6, also crossed onto Dutton's Flint Inbred (5 and 6), (freezing injury, poor germination); 3 ears
- " 40-83 (x) and # PWR Y gs?, seg. fl?, may seg. v6, also pollinated with Inbred I (1 and 2); 6 ears
- " 40-84 # PWR cr_x, seg. y sk, may seg. d_x bl_x v_x, also pollinated with Inbred I (1) and reciprocally with Dutton's Flint Inbred (5 and 6); 2 ears
- " 40-88 (x) Seg. Pr pr, may seg. yg_a, also pollinated with Inbred II (3) and Dutton's Flint Inbred (5) and reciprocally with Inbred I (1); 6 ears
- " 40-89 (x) Y, seg. pr wx, may seg. d_a, also pollinated with Inbred I (1); 7 ears
- " 40-91 (x) and # lg_x, seg. y, may seg. pg_x; 3 ears
- " 40-92 (x) Y wx?, seg. su, may seg. ar_a, also pollinated with Inbred II (3); 4 ears
- " 40-93 (x) Y wx?, seg. Pr pr su, may seg. ar_a, also crossed onto Dutton's Flint Inbred (6); 4 ears
- " 40-94 (x) Seg. Pr pr su wx?, may seg. pg_a, also pollinated with Inbred II (3), and reciprocally with Inbred I (2) and Inbred II (3 and 4); 7 ears
- " 40-95 (x) and # PWR Y cr, seg. wx pg2 "white stripe", may seg. lg_x, also pollinated with Inbred I (1 and 2) and reciprocally with Inbred I (1) and Inbred II (3); 7 ears
- " 40-96 (x) A Pl, seg. y Pr pr lg gl2 B v4, may seg. ts_x; 3 ears
- " 40-98 (x) y Hadjinov's gl5, seg. v_x, also pollinated with Inbred II (3) and reciprocally with Inbred I (1); few seeds

- Co 40-99 (x) y Hadjinov's gl6; few seeds
- " 40-100 (x) y, may seg. Hadjinov's gl7; 3 ears
- " 40-101 (x) Seg. y B Pl f, may seg. wx Hadjinov's gl8, also
pollinated with Inbred I (2) and
reciprocally with Inbred I (1)
and Dutton's Flint Inbred (6);
3 ears
- " 40-102 (x) P Y Hadjinov's gl10, also pollinated with Inbred
I (1 and 2) and Inbred II (3);
4 ears
- " 40-103 (x) and # "Deep Y" lg gl4, may seg. v_x bm_x, also
pollinated with Inbred I (1 and 2),
and reciprocally with Dutton's
Flint Inbred (5 and 6); 9 ears
- " 40-105 (x) and # Y, seg. rs2 gl_x; 5 ears
- " 40-107 (x) and # Seg. y Pr I? Hadjinov's at si ts2 br? bv?,
may seg. f, also pollinated with
Inbred I (1 and 2) and reciprocal-
ly with Inbred I (1); 6 ears
- " 40-108 (x) P^{Wr} Y, may seg. Hadjinov's bs v_x; 1 ear
- " 40-109 (x) and # Y A b Pl, seg. P vb, may seg. v_x, also
pollinated with Inbred I (1) and
reciprocally with Inbred I (1);
6 ears
- " 40-110 (x) and # y A Pl (zg3) lg_x, seg. B d_x, also pol-
linated with Inbred I (1); 7 ears
- " 40-111 # A, seg. y Pr Rgg su B Pl ba, may seg. v_x, also
pollinated with Inbred I (2);
11 ears
- " 40-112 (x) and # A su^{am}?, seg. y Pr pr Pl ba2 v_x f? lg_x,
also pollinated with Inbred II
(3) and reciprocally with Inbred
I (1); 6 ears
- " 40-113 (x) and # y a lg_x, seg. ts4 g_x cr_x, may seg. v_x,
also pollinated with Inbred I (1);
8 ears
- " 40-114 Crossed onto Inbred I (2), may seg. d_x^s d^D
- " 40-115 (x) P^{Wr}, seg. y Pr pr Rgg Rn^j? su B Pl lg_x^x, may seg.
g d7 v_x, also crossed onto Inbred
I (1) and Dutton's Flint Inbred
(5); 15 ears
- " 40-116 (x) and # y a C r pr wx, may seg. ys_x, also pollin-
ated with Inbred I (1) and Inbred
II (3) and reciprocally with In-
bred I (2); 6 ears
- " 40-117 (x) and # Seg. y Bn v5 gl, may seg. ws2; 5 ears
- " 40-118 (x) and # Seg. P^{Wr} y Pr pr c sh wx ws gl4, also
crossed onto Inbred I (1); 6 ears
- " 40-119 (x) and # Seg. y Pr pr g?, may seg. li ws2, also
crossed onto Inbred I (1); 4 ears
- " 40-120 (x) a B Pl wx?, seg. y as lg_x "white stripe", may
seg. gs, also pollinated with In-
bred I (1); 5 ears
- " 40-121 (x) and # Seg. Pr pr po; 10 ears

- Co 40-122 (x) Y, may seg. st v_x; 2 ears
 " 40-123 (x) P a, may seg. br f bm2 nl2 w_x, also crossed onto Inbred I (2); 2 ears
 " 40-124 (x) and # Y, seg. Pr pr Pl Rg rt bl?, may seg. d_x, also crossed onto Inbred I (1 and 2), Inbred II (3) and Dutton's Flint Inbred (5 and 6); 5 ears
 " 40-125 (x) and # P^{VV} - bm2/lg-b/y?-pl/ c-wx/g - R^{gg}/j/pr pk?; few seeds
 " 40-126 (x) and # P^{VV} and p-bm2/lg-b/A-Cr cr + cr/Su and su/y? - pl/c-wx/g - R^{gg}/pr/j; few seeds
 " 40-127 (x) Seg. P^W y Pr vp5, also pollinated with Inbred I (2); 8 ears
 " 40-128 (x) P^W y o2 v5 ra gl; 1 ear
 " 40-129 (x) P^W A B pl d^s? an_x, seg. y Bn? Lg3?, also crossed onto Inbred I (2); 2 ears
 " 40-130 (x) Rg d^s? an_x, seg. y; few seeds
 " 40-131 (x) Y, seg. su? bt?, also open pollinated ear somewhat like Tp; few seeds
 " 40-133 (x) y pr, seg. Rst? wx? g, may seg. mr; 3 ears
 " 40-134 (x) and # P A br f bm2, may seg. ts2; 3 ears
 " 40-135 (x) Seg. y⁴ y_x It Pr pr; 5 ears
 " 40-136 (x) Hadjinov's gl6, seg. y Wh?; 3 ears

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- Co 41-1 Inbred I (U.S. 204) P^W Y A b pl, pollinated with Y A b pl nl, seg. R, may seg. d_x g zb5 (113); y gl10, may seg. w_x (69); Y a lg2 ra2 ? (21); Y cr na a v5 gl, may seg. lg_x (54); Y A b pl su vl4, may seg. sh d3 (166); P Y A b pl, may seg. d5 v5 (57); Y A b pl, seg. hf, may seg. wx v_x Rg? (78); Y A b pl rs2, may seg. gl_x v_x (12); A b Pl Kn (86); Y A b pl gs_x, seg. msl1, may seg. lg_x "ar-like" stripe (103); y A b pl vl8, may seg. l4 (91); y A b pl pg2, seg. d (128); may seg. vp v? (171); pr A b Pl bm ys, may seg. v2 (180); "small anthers", may seg. pr su (170); nl2, may seg. br f bm2 gl_x (116); Y A b pl Rs, may seg. gl_x (13); Y A b pl cr_x, may seg. vp4 (174); Y A b pl bl_x (47); bv?, may seg. g pg (126); pr A b pl v3?, may seg. su (156); Y A B pl lg pk?, may seg. pg_x bm_x "white stripe" (132); Y a na yt, may seg. ts4 (182); Y A b pl d^s, seg. an_x (14); 28 ears
 " 41-2 (x) Inbred II (West Branch) Y A b pl, also pollinated with Y A b pl nl, seg. R, may seg. d_x g zb5 (113); Y A B pl lg bm_x pk?, may seg. pg_x "white stripe" (132); pr A b Pl bm v2, may seg. ys (180); 4 ears
 " 41-3 (x) y A b pl, may seg. g3 l_x; 1 ear
 " 41-7 (x) P sh A B pl, may seg. l6; 1 ear
 " 41-9 (x) y su A b pl "yellow flecked leaves", may seg. v8 d_x; 1 ear
 " 41-10 # Bn? A b pl cr?, may seg. v6 d_x; 1 ear

- Co 41-11 (x) and # y A b pl Hadjinov's gl₆; 3 ears
- " 41-12 # Y A b pl, seg. rs₂, may seg. gl_x v_x, also crossed onto Inbred I(1); 3 ears
- " 41-13 (x) and # A b pl Rs, seg. y, may seg. gl_x, also crossed onto Inbred I(1); 2 ears
- " 41-14 # Y A b pl d^s an_x, also crossed onto Inbred I(1); 3 ears
- " 41-15 (x) and # A b pl gl₄, seg. y Pr pr wx? ws; 7 ears
- " 41-16 # PVV - bm₂/lg-b/y-pl/c-wx/g-R^{gg}/j/pr pk?, also pollinated with 17, same genotype; 5 ears
- " 41-17 (x) and # P^{VV} - bm₂/lg-b/y-pl/c-wx/g-R^{gg}/j/pr pk?; 5 ears
- " 41-19 (x) and # Y A b pl, seg. Pr pr su_x h?; 3 ears
- " 41-20 (x) and # Y a C R pr in wx; 6 ears
- " 41-21 # Y a lg₂ ra₂?, also pollinated with Y a C R pr in wx (20), and with Inbred I (1), and reciprocally with Inbred I (1); 4 ears
- " 41-22 Y a C R Pr B Pl pollinated with Y a lg₂ ra₂? (21); 1 ear
- " 41-23 (x) and # y su a Dt, may seg. lg₂; 4 ears
- " 41-24 (x) and # y a₂ A C R v₂, seg. P^Wr, may seg. bm; 4 ears
- " 41-25 # y a₂ A C R pr bt bv; 5 ears
- " 41-26 (x) and # y a₃ (A B pl?) Og; 3 ears may
- " 41-28 (x) and # Seg. P^Wr y su Ts₆ al? ij?/seg. gl_x; 6 ears
- " 41-29 (x) and # P^Wr Y A b pl, may seg. an₂ v_x gl_x d_x; 6 ears
- " 41-30 (x) and # Y wx, seg. ar; 9 ears
- " 41-31 # Y wx da A b pl ar sa, seg. Pr pr; 3 ears
- " 41-32 (x) and # y, seg. P^{VV} B z₁ as, may seg. ms₁₇; 6 ears
- " 41-33 (x) and # y Pr, seg. B R^{gg} ms₁₇ as, may seg. z₁; 9 ears
- " 41-34 # Seg. y at si bl_x ts_x f fl?, may seg. bv br zb_x v_x gl_x; 3 ears
- " 41-35 Y sh A b pl au au₂ cr_x, pollinated with Inbred I (1), may seg. vp?; 3 ears (includes 2 very small ears)
- " 41-36 (x) and # Pr S_x A B pl R^{gg} lg_x bm_x; 2 ears
- " 41-37 (x) and # y Pr A B pl C R^{gg} S_x lg bm₂, seg. g? v? may seg. j d cr ts₂; 10 ears
- " 41-38 # Y a B Pl C R Pr, may seg. v_x; 4 ears
- " 41-39 # PCW A b pl, may seg. ba_x; 1 ear
- " 41-40 (x) P A pl, seg. y su B ba, may seg. ba_x v_x; 16 ears
- " 41-41 (x) P Y A Pl, seg. Pr su B ba₂, may seg. ba_x v_x; 18 ears
- " 41-42 # Y gl₁ ij, seg. P bd; 2 ears
- " 41-43 (x) and # A b, seg. y Pl ra gl₁ ij bd; 10 ears
- " 41-44 (x) and # Y A b pl bk gl_x; 3 ears
- " 41-45 (x) and # Y bk₂; 5 ears
- " 41-46 # P Y A b pl, seg. sk lg_x, may seg. d_x v_x bl? cr?; 1 ear
- " 41-47 Y A b pl bl_x, crossed onto Inbred I (1)
- " 41-48 # A B Pl lg_x, seg. y Pr sk_x, may seg. R^{gg} bm; 1 ear
- " 41-49 (x) and # y a₂ A C R b pl v₂, seg. P^Wr; 15 ears
- " 41-51 (x) and # Y, seg. P^Wr sh wx v_x, may seg. bp zb?; 17 ears

- Co 41-52 # PWR Y A b pl bt2, may seg. gl_x "white stripe", 1 ear
- " 41-53 (x) and # y c, seg. su, may seg. v9; 3 ears
- " 41-54 Y cr na a v5 gl, crossed onto Inbred I (1), may seg. lg
- " 41-55 Y A b pl, pollinated with Inbred I (1), seg. PWR Tu dH "white stripe", may seg. su; 3 ears
- " 41-56 (x) and # P Y sh wx c, may seg. d3; 4 ears
- " 41-57 P Y A b pl, crossed onto Inbred I (1), may seg. d5 v5
- " 41-58 (x) and # Y wx?, seg. nl?, may seg. d_b ms?; 2 ears
- " 41-60 Y de A b pl, pollinated with Inbred I (1), seg. ml?; 2 poor seeds
- " 41-61 (x) and # y a Dt lg, seg. ts4 na su, may seg. g; 6 ears
- " 41-62 # PWR Y fl2 gl_x; 2 ears
- " 41-63 (x) and # gl 1j, seg. y, may seg. ra fr fr2; 11 ears
- " 41-65 (x) and # y A b pl Og li g; 2 ears
- " 41-67 (x) and # Y, seg. su, may seg. Ga; 6 ears
- " 41-68 (x) PWR Y wx gl3 cr_x, seg. su, may seg. wl, also pollinated with Inbred I (1); 3 ears
- " 41-69 # y gl10, may seg. wx, also crossed onto Inbred I (1); 2 ears
- " 41-72 (x) and # y A b pl gl6, seg. P?; 3 ears
- " 41-74 (x) and # y A b pl, seg. gl7 vl7 Hadjinov's gl7, may seg. "white stripe"; 4 ears
- " 41-75 (x) PWR Y A b pl, seg. gl9; 1 ear
- " 41-76 (x) and # Seg. PWR y lg v4 gs2, may seg. gl2; 15 ears
- " 41-77 PWR Y A b pl h, pollinated with Inbred I (1); few seeds
- " 41-78 (x) and # PWR Y A b pl, seg. wx hf vx, may seg. Rg?, also crossed onto Inbred I (1); 3 ears
- " 41-79 # y A b pl Hs; 2 ears
- " 41-80 # y A c Rgg pr in su, seg. PVV sh wx, may seg. vx; 3 ears
- " 41-82 (x) and # Seg. y4 and or y_x It Pr, may seg. sr_x; 6 ears
- " 41-83 y4 It It a c r pr i pollinated with Inbred I (1); 1 ear
- " 41-84 (x) and # A b pl, seg. y sh Wc? ms8 j gl_x, may seg. vl6; 4 ears
- " 41-85 (x) and # Y A b pl gl3, seg. su, may seg. j2; 5 ears
- " 41-86 # A, seg. y B Pl Kn, also crossed onto Inbred I (1); 3 ears
- " 41-87 (x) P A B pl lg_x bk?, may seg. l w; 1 ear
- " 41-88 (x) and # r, seg. y su Pl "white stripe", may seg. g 12; 8 ears
- " 41-89 # PWR Y "white stripe", may seg. l3; few seeds
- " 41-90 (x) and # PWR Y "white stripe" li?, seg. Pr, may seg. l3; 4 ears
- " 41-91 y A b pl vl8, may seg. l4, pollinated with Inbred I (1) and reciprocally with Inbred I (1); few seeds
- " 41-92 PWR Y A b pl, may seg. sh l7 ms2, pollinated with Inbred I (1); 2 ears

- Co 41-93 (x) Y su A B pl Ts5?, may seg. 1a; 1 ear; also su A B pl 1a pollinated with (94) su A B pl Ts5 1a lg_x, may seg. gl_x; few seeds
- " 41-95 (x) PWR Wc? A b pl gl_x, seg. y, may seg. ms_x; 2 ears
- " 41-97 (x) and # A b Pl, seg. PWR Pr pr Rst r fl? may seg. g mr "white stripe"; 2 ears
- " 41-98 Y A b pl, seg. PWR ms2, may seg. 17 br_x, pollinated with Inbred I (1); 2 ears
- " 41-99 P A b pl, seg. ms5, may seg. lg_x, pollinated with Inbred I (1); 1 ear
- " 41-100 (x) and # P Y A B pl, seg. Pr pr ms6, may seg. g_x; 4 ears
- " 41-101 # A b pl, seg. y ms9; 2 ears
- " 41-102 # PWR, seg. ms10 "white stripe", also pollinated with Inbred I (1); 3 ears
- " 41-103 # Y, seg. P ms11 gs_x, may seg. lg_x, "ar-like stripe", also crossed onto Inbred I (1); 2 ears
- " 41-104 (x) Y A b pl, may seg. ms12 bm_x "white stripe" v?; 1 ear
- " 41-105 # y, seg. ms13; 4 ears
- " 41-106 # Y, seg. wx sh ms14; 4 ears
- " 41-107 (x) and # PWR, seg. Pr pr bm, may seg. ms18 l_x lg_x d_x; 2 ears
- " 41-109 (x) and # P b Pl, seg. Ab? ms37; 5 ears
- " 41-111 PWR y A b pl, may seg. vl9 ms_x, pollinated with Inbred I (1); 2 ears
- " 41-112 # Seg. PWR y Pr pr su B Pl na2, may seg. "white stripe"; 2 ears
- " 41-113 # Y A b pl nl, seg. r Pr, may seg. g zb5 d_x, also crossed onto Inbred I (1) and Inbred II (2); few seeds
- " 41-114 # P Pr A b pl g, may seg. nl zb5 gl_x, also pollinated with (113) Y A b pl nl; 2 ears
- " 41-115 (x) and # PWR y A b pl r zb5, may seg. nl g; 7 ears
- " 41-116 (x) and # a, seg. P br f bm2, may seg. nl2 gl_x, also crossed onto Inbred I (1); 5 ears
- " 41-117 # Y o A B pl, seg. vx; 5 ears
- " 41-118 PWR y o2 A b pl, pollinated with Inbred I (1); 1 ear
- " 41-119 # P A b Pl sm, seg. py; 1 ear
- " 41-120 (x) Seg. Pr pr zb? pg? pb?, may seg. ms_x and usually completely sterile plants with necrotic leaves; 1 ear
- " 41-122 (x) and # y A b pl pb4, seg. gl_x; 7 ears
- " 41-123 (x) Y wx, may seg. pb_x lg_x "white stripe"; 1 ear
- " 41-124 # PWR, seg. y B pb_x, also pollinated with Inbred I (1); 2 ears
- " 41-126 # PWR Pr bv?, may seg. g pg, also crossed onto Inbred I (1); few seeds
- " 41-128 # y A b pl, seg. pg2 d, also crossed onto Inbred I (1); 6 ears
- " 41-129 (x) Pr, seg. su, may seg. pga; 2 ears
- " 41-130 (x) and # y A b pl, seg. lg_x; 8 ears
- " 41-131 (x) and # y lg_x, seg. pg_x; 11 ears

- Co 41-132 (x) and # Y lg pk?, seg. B "white stripe", may seg. pg_x bm_x, also crossed onto Inbred I (1) and Inbred II (2); 4 ears
- " 41-133 # Pw^r y A b pl bm, may seg. pg_x msl8 lg_x "white stripe", also pollinated with Inbred I (1); 6 ears
- " 41-134 # Pw^r, seg. y pm lg2; 9 ears
- " 41-135 # pr A b Pl; 4 ears
- " 41-136 (x) and # A b pl R88 Pr; 5 ears
- " 41-137 # P A b pl, seg. ra2?; 2 ears
- " 41-138 (x) and # P, seg. Pr a lg2 ra2 ra_x; 9 ears
- " 41-139 (x) and # Seg. y lg_x gl_x d_x "light green", may seg. w_x v4; 12 ears
- " 41-140 # y su2 lg_x, seg. Pw^r sb ms?; 5 ears
- " 41-141 y A b pl sb pk?, may seg. sh, pollinated with Inbred I (1); 1 ear
- " 41-142 (x) and # Seg. pcr pcw y sb ms_x; 6 ears
- " 41-143 # Y bl_x, seg. Pr si at br f bv? ts2?, may seg. v_x gl_x, also pollinated with Inbred I (1); 7 ears
- " 41-145 (x) and # y A b pl sr bm2, seg. Pw^r Pr an; 10 ears
- " 41-146 # Pw^r o2 A b pl v5 ra gl, seg. y; 6 ears
- " 41-147 # Y A b pl, may seg. st; 4 ears
- " 41-148 # su^{am} du A b pl, seg. y; 6 ears
- " 41-149 # sy A b Pl, seg. y, may seg. al; few seeds
- " 41-150 (x) and # A b pl, seg. Bn? tn v_x d_x; 5 small ears
- " 41-151 # y ra gl v5, also pollinated with Inbred I (1); 2 ears
- " 41-152 # v5 gl, seg. y Pr pr wx? ra Tp; 3 ears
- " 41-153 (x) and # A, seg. y su R88 Pr pr Bn? v5 ra gl Tp B Pl; 6 ears
- " 41-154 # P br f bm2, seg. a, may seg. ts2; 2 ears
- " 41-155 (x) and # y, seg. Pr Mt? tw3 g_x sr_x gl_x, may seg. bl_x, 7 ears
- " 41-156 # pr A b pl v3?, may seg. su, also crossed onto Inbred I (1); 1 ear
- " 41-157 (x) and # A b pl, seg. y Pr pr v3, may seg. v_x; 4 ears
- " 41-158 # Pw^r Y A b pl v7-striped; 2 ears
- " 41-159 (x) and # Pw^r Y A b pl, seg. v7-striped; 4 ears
- " 41-160 # y vl2, seg. pr, may seg. lg_x, also pollinated with Inbred I (1); 4 ears
- " 41-161 (x) and # Seg. y Pr pr Pl vl3; 11 ears
- " 41-163 # Y su A b pl, may seg. sp l_x; 1 ear
- " 41-164 (x) and # Seg. P y su, may seg. sp; 7 ears
- " 41-166 (x) and # Y su A b pl vl4, seg. sh, may seg. d3, also crossed onto Inbred I (1); 2 ears
- " 41-167 (x) and # wx? l1, seg. y su Pl, may seg. w_x; 10 ears
- " 41-168 (x) Pw^r Y v20 lg_x, also pollinated with Inbred I (1); 4 ears
- " 41-169 (x) and # P y A b pl, seg. va2, also pollinated with Inbred I (1); 6 ears
- " 41-170 "small anthers", may seg. pr su, crossed onto Inbred I (1)
- " 41-171 (x) y Pr A b pl, seg. r vp, may seg. v_x, also crossed onto Inbred I (1); 1 ear
- " 41-172 (x) pr v_x pk?, seg. vp2?, may seg. bm_x; 4 ears

- Co 41-173 (x) pr pk?, seg. vp2?, may seg. v_x bm_x; 2 ears
 " 41-174 (x) and # Pw^r Y A b pl cr_x, seg. vp4?, also crossed onto Inbred I (1); 2 ears
 " 41-175 Pw^r Y A b pl cr_x, may seg. sh vp4, pollinated with Inbred I (1); 2 ears
 " 41-176 (x) and # P^v y A, seg. wa "white stripe" BW? Pl; 3 ears
 " 41-177 # Y Wc A b pl, may seg. "white stripe"; 1 ear
 " 41-178 # A b pl, seg. y Pr pr Mt? g li ws2; 11 ears
 " 41-179 (x) and # Y Y A B pl, seg. y_x, may seg. w_x al; 4 ears
 " 41-180 # pr bm, seg. y Mt? sh wx ys v2 Pl, also crossed onto Inbred I (1) and Inbred II (2); 3 ears
 " 41-181 (x) and # y a C r pr wx, may seg. ys_x; 3 ears
 " 41-182 # Y wx a yt, seg. na, may seg. ts4, also pollinated with Inbred I (1) and reciprocally with Inbred I (1); 3 ears
 " 41-183 # Y A b pl zb4; 2 ears
 " 41-184 (x) Pw^r Y A b pl, seg. zb4; 2 ears
 " 41-185 (x) and # Y A b pl, seg. zb4; 4 ears
 " 41-187 (x) and # Y T8-9 homozygous terminal number 9 knob, seg. B Pl also R^{gg} or r^{gg}; 6 ears
 " 41-191 (x) and # y T1-2; 2 ears
 " 41-192 (x) and # y A pl T1-2b, seg. Pw^r Pr pr B, may seg. v_x; 3 ears
 " 41-194 # a2 bm bt pr A A C C R R; 133 seeds
 " 41-195 (x) a2 bt pr, seg. y bm; 1 ear

J. E. Welch

Trisomic stocks

The program began by Randolph in 1940 of improving and building up reserve stocks of all the available trisomes was continued in the summer of 1941. Trisomes one and four are still missing.

Root tip counts were made on over 1500 plants to determine the trisomic plants. Over 300 ears were harvested.

In making crosses several inbred stocks were used as well as different genetic tester stocks. These were all checked to make sure that no B chromosomes were present.

Selected ears have been turned over to the Coöp. and are here listed under Coop. numbers.

- Co 41-196 No. 2 trisome x Luce's Favorite Inbred
 1. (x) - 2 ears
 2. x L. F. Inbred - 5 ears
 3. x lg - 2 ears

- Co 41-197 No. 2 trisome x Cornell 11 Inbred
 1. (x) - 4 ears
 2. x L.F. Inbred - 1 ear
 3. # - 3 ears
- " 41-198 No. 2 trisome x Inbred II (West Branch)
 1. (x) - 1 ear
 2. x L.F. - 3 ears
 3. # - 1 ear
- " 41-199 No. 2 trisome x lg
 1. x L.F. - 4 ears
 2. # - 2 ears
- " 41-200 No. 3 trisome x lg2
 1. (x) - 6 ears
 2. x L.F. - 2 ears
 3. # - 3 ears
- " 41-201 No. 3 trisome x L.F. Inbred
 1. x L.F. - 2 ears
- " 41-202 No. 3 trisome x Inbred II
 1. x L.F. - 3 ears
- " 41-203 No. 5 trisome x Inbred II
 1. (x) - 1 ear
 2. x L.F. - 5 ears
 3. x bt - 2 ears
- " 41-204 No. 6 trisome x su2
 1. (x) - 3 ears
 2. x L.F. - 5 ears
 3. # - 2 ears
- " 41-205 No. 7 trisome x L.F. Inbred
 1. x L.F. 2 ears (all ears of trisome 7 poor)
- " 41-206 No. 7 trisome x Inbred II
 1. x L.F. - 2 ears
 2. x gl - 1 ear
 3. open - 1 ear
- " 41-207 No. 8 trisome x L.F. Inbred
 1. (x) - 2 ears
 2. x L.F. - 5 ears
 3. # - 2 ears
- " 41-208 No. 8 trisome x j
 1. (x) - 2 ears
 2. # - 2 ears
- " 41-209 No. 9 trisome x wx (No. 9 also wx)
 1. (x) - 2 ears
 2. x L.F. - 4 ears
 3. # 1 ear
- " 41-210 No. 10 trisome x L.F. Inbred
 1. (x) - 1 ear
 2. x L.F. - 4 ears
 3. x vl8 - 2 ears
- " 41-211 No. 10 trisome x vl8
 1. (x) - 2 ears
 2. x L.F. - 2 ears

John Einset

V. Index of Seed Stocks Propagated in 1940 and 1941

A complete index of all Coöp stocks on hand at the close of the 1939 season appeared in the 1940 News Letter. The culture number of an inbred is followed by the number in parenthesis of the male parent carrying the gene in question. m.s. = may segregate.

a	Co	40-1 (71), 40-2 (71), 40-2 (116), 40-2 (123), 40-26, 40-70, 40-71, 40-72, 40-73, 40-113, 40-116, 40-120, 40-123, 41-1 (21), 41-1 (54), 41-1 (182), 41-20, 41-21, 41-22, 41-23, 41-38, 41-61, 41-83, 41-116, 41-138, 41-154, 41-181, 41-182
a ^p	"	40-18, 40-43
Ab?	"	41-109
a2	"	41-24, 41-25, 41-49, 41-194, 41-195
a3	"	41-26
a1	"	41-149 (m.s.), 41-179 (m.s.)
a1?	"	41-28
an	"	41-145
an2	"	41-29 (m.s.)
anx	"	40-2 (81, m.s.), 40-2 (129, m.s.), 40-25, 40-81, 40-129, 40-130, 41-1 (14), 41-14
"anthers small"	Co	41-1 (170)
ar	Co	41-30, 41-31
ara	"	40-6 (93, m.s.), 40-92 (m.s.), 40-93 (m.s.)
as	"	40-120, 41-32, 41-33
at	"	40-1 (107), 40-107, 41-34, 41-143
au	"	41-35
au2	"	41-35
B	"	40-1 (101, m.s.), 40-1 (69), 40-1 (115, m.s.), 40-2 (129), 40-3 (69), 40-5 (115, m.s.), 40-5 (69), 40-6 (101, m.s.), 40-17, 40-18, 40-43, 40-51, 40-69, 40-73, 40-76, 40-96, 40-101, 40-110, 40-111, 40-115, 40-120, 40-129, 41-7, 41-22, 41-32, 41-33, 41-36, 41-37, 41-38, 41-40, 41-41, 41-48, 41-86, 41-87, 41-93, 41-100, 41-112, 41-117, 41-124, 41-132, 41-153, 41-179, 41-187, 41-192
BW?	"	41-176
ba	"	40-111, 41-40
ba2	"	40-1 (112), 40-112, 41-41
ba _x	"	41-39 (m.s.), 41-40 (m.s.), 41-41 (m.s.)
bd	"	41-42, 41-43
bk	"	41-44
bk2	"	41-45
bk?	"	41-87
bl _x	"	40-5 (84, m.s.), 40-6 (84, m.s.), 40-84 (m.s.), 41-1 (47), 41-34, 41-143, 41-155 (m.s.)
bl?	"	40-1 (124, m.s.), 40-2 (124, m.s.), 40-3 (124, m.s.), 40-5 (124, m.s.), 40-6 (124, m.s.), 40-124, 41-46 (m.s.)
bm	"	40-62, 41-1 (180), 41-2 (180), 41-24 (m.s.), 41-48 (m.s.), 41-107, 41-133, 41-180, 41-194, 41-195

bm2 Co 40-2 (123, m.s.), 40-21, 40-45, 40-123 (m.s.),
 40-125, 40-126, 40-134, 41-1 (116, m.s.), 41-16,
 41-17, 41-37, 41-116, 41-145, 41-154
 bm3 " 40-54, 40-57
 bmX " 40-1 (69), 40-3 (69), 40-5 (103, m.s.), 40-6 (103,
 m.s.), 40-5 (69), 40-69, 40-103 (m.s.), 41-1 (132,
 m.s.), 41-2 (132), 41-36, 41-104 (m.s.), 41-132
 (m.s.), 41-172 (m.s.), 41-173 (m.s.)
 Bn " 40-117
 Bn? " 40-2 (81, m.s.), 40-2 (129, m.s.), 40-5 (82, m.s.),
 40-6 (82, m.s.), 40-81, 40-82, 40-129, 41-10,
 41-150, 41-153
 bp " 41-51 (m.s.)
 br " 40-1 (107, m.s.), 40-2 (123), 40-21, 40-45, 40-123
 (m.s.), 40-134, 41-1 (116, m.s.), 41-34 (m.s.),
 41-116, 41-143, 41-154
 brX " 41-98 (m.s.)
 br? " 40-107
 bs Hadjinov Co 40-108 (m.s.)
 bs? Co 40-67 (m.s.), 41-120 (m.s.)
 bt " 41-25, 41-194, 41-195
 bt2 " 41-52
 bt? " 40-131
 bv " 40-1 (107, m.s.), 41-25, 41-34 (m.s.)
 bv? " 40-107 41-1 (126), 41-126, 41-143
 c " 40-1 (118, m.s.), 40-118, 40-125, 40-126, 41-16,
 41-17, 41-53, 41-56, 41-80, 41-83
 cr " 40-1 (95), 40-3 (95), 40-95, 40-126, 41-1 (54),
 41-37 (m.s.)
 crX " 40-2 (81, m.s.), 40-5 (82), 40-6 (82), 40-5 (84,
 m.s.), 40-6 (84, m.s.), 40-76, 40-78, 40-81 (m.s.),
 40-82, 40-84, 40-113, 41-1 (174), 41-35, 41-68,
 41-174, 41-175
 cr? " 41-10, 41-46 (m.s.)
 d " 40-2 (114, m.s.), 40-2 (129), 40-25, 40-26, 40-48,
 40-129 (?), 40-130 (?), 41-1 (128), 41-1 (14),
 41-14, 41-37 (m.s.), 41-128
 d3 " 40-75 (m.s.), 41-1 (166, m.s.), 41-56 (m.s.),
 41-166 (m.s.)
 d5 " 41-1 (57, m.s.)
 d7 " 40-1 (115, m.s.), 40-5 (115, m.s.), 40-115 (m.s.)
 da " 40-89 (m.s.)
 db " 41-58 (m.s.)
 dH " 41-55
 dx " 40-1 (124, m.s.), 40-2 (124, m.s.), 40-1 (74, m.s.),
 40-2 (81, m.s.), 40-2 (114, m.s.), 40-3 (124, m.s.),
 40-5 (124, m.s.), 40-6 (124, m.s.), 40-5 (74, m.s.),
 40-5 (82, m.s.), 40-6 (82, m.s.), 40-5 (84, m.s.),
 40-6 (84, m.s.), 40-74 (m.s.), 40-77 (m.s.), 40-78
 (m.s.), 40-79 (m.s.), 40-80 (m.s.), 40-81, 40-82
 (m.s.), 40-84 (m.s.), 40-110, 40-124 (m.s.), 41-1
 (113, m.s.), 41-2 (113, m.s.), 41-9 (m.s.), 41-10
 (m.s.), 41-29 (m.s.), 41-46 (m.s.), 41-107 (m.s.),
 41-113 (m.s.), 41-139, 41-150
 da " 41-31

de	Co	41-60
Dt	"	41-23, 41-61
du	"	41-148
f	"	40-1 (101, m.s.), 40-1 (107, m.s.), 40-1 (71), 40-2 (71), 40-2 (123), 40-6 (101), 40-21, 40-45, 40-71, 40-72, 40-101, 40-107 (m.s.), 40-123 (m.s.), 40-134, 41-1 (116, m.s.), 41-34, 41-116, 41-143, 41-154
fx	"	40-1 (74), 40-5 (74), 40-74 (m.s.), 40-79
f?	"	40-1 (112, m.s.), 40-112
fl	"	40-24, 40-47
fl2	"	41-62
flx	"	40-78, 40-80
fl?	"	40-83, 41-34, 41-97
fr	"	41-63 (m.s.)
fr2	"	41-63 (m.s.)
fs	"	40-20, 40-44
g	"	40-1 (115, m.s.), 40-1 (119, m.s.), 40-4 (65, m.s.), 40-5 (115, m.s.), 40-30 (m.s.), 40-65, 40-66, 40-115 (m.s.), 40-125, 40-126, 40-133, 41-1 (113, m.s.), 41-1 (126, m.s.), 41-2 (113, m.s.), 41-16, 41-17, 41-61 (m.s.), 41-65, 41-88 (m.s.), 41-97 (m.s.), 41-113 (m.s.), 41-114, 41-115 (m.s.), 41-126 (m.s.), 41-178
g3	"	40-60 (m.s.), 41-3 (m.s.)
g4	"	40-52, 40-55, 40-58, 40-59
gx	"	40-113, 41-100 (m.s.), 41-155
g?	"	40-119, 41-37
Ga	"	41-67 (m.s.)
gl	"	40-63, 40-117, 40-128, 41-1 (54), 41-42, 41-43, 41-63, 41-146, 41-151, 41-152, 41-153
gl2	"	40-22, 40-23, 40-24, 40-46, 40-47, 40-96, 41-76 (m.s.)
gl3	"	41-68, 41-85
gl4	"	40-1 (118), 40-5 (103), 40-6 (103), 40-27, 40-28, 40-29, 40-49, 40-50, 40-103, 40-118, 41-15
gl6	"	41-72
gl7	"	41-74
gl9	"	41-75
gl10	"	41-1 (69), 41-69
gl5 Hadjinov	Co	40-1 (98), 40-98
gl6 Hadjinov	"	40-99, 40-136, 41-11
gl7 Hadjinov	"	40-100 (m.s.), 41-74
gl8 Hadjinov	"	40-1 (101, m.s.), 40-6 (101, m.s.), 40-101 (m.s.)
gl10 Hadjonov	"	40-102
glx	Co	40-105, 41-1 (12, m.s.), 41-1 (116, m.s.), 41-1 (13, m.s.), 41-12 (m.s.), 41-13 (m.s.), 41-28 (m.s.), 41-29 (m.s.), 41-34 (m.s.), 41-44, 41-52 (m.s.), 41-62, 41-84, 41-93 (m.s.), 41-95, 41-114 (m.s.), 41-116 (m.s.), 41-122, 41-139, 41-143 (m.s.), 41-155
gs	"	40-120 (m.s.)
gs2	"	41-76
gsx	"	41-1 (103), 41-103
gs?	"	40-83
h	"	41-77

h?	Co	41-19
hf	"	41-1 (78), 41-78
Hs	"	41-79
I?	"	40-1 (107, m.s.), 40-107
ij	"	41-42, 41-43, 41-63
ij?	"	41-28
in	"	40-70, 41-20, 41-80
It	"	40-135, 41-82, 41-83
j	"	40-11 (m.s.), 40-36 (m.s.), 40-70, 40-125, 40-126, 41-16, 41-17, 41-37 (m.s.), 41-84
j2	"	41-85 (m.s.)
Kn	"	41-1 (86), 41-86
Knob	"	41-187
l	"	41-87 (m.s.)
l2	"	40-66 (m.s.), 41-88 (m.s.)
l3	"	41-89 (m.s.), 41-90 (m.s.)
l4	"	41-1 (91, m.s.), 41-91 (m.s.)
l6	"	40-76 (m.s.), 41-7 (m.s.)
l7	"	41-92 (m.s.), 41-98 (m.s.)
lx	"	40-1 (64, m.s.), 40-5 (64, m.s.), 40-60 (m.s.), 40-62 (m.s.), 40-64 (m.s.), 40-68 (m.s.), 41-3 (m.s.), 41-107 (m.s.), 41-163 (m.s.)
la	"	41-93
lg	"	40-1 (69), 40-3 (69), 40-5 (103), 40-6 (103), 40-5 (69), 40-22, 40-23, 40-24, 40-28, 40-46, 40-47, 40-49, 40-69, 40-70, 40-72, 40-73, 40-96, 40-103, 40-125, 40-126, 41-1 (132), 41-2 (132), 41-16, 41-17, 41-37, 41-61, 41-76, 41-132
lg2	"	40-25, 40-26, 40-48, 41-1 (21), 41-21, 41-22, 41-23 (m.s.), 41-134, 41-138
Lg3	"	40-2 (129)
Lg3?	"	40-129
lgx	"	40-1 (95, m.s.), 40-1 (115, m.s.), 40-1 (112, m.s.), 40-1 (71), 40-2 (71), 40-1 (64, m.s.), 40-3 (95, m.s.), 40-5 (115, m.s.), 40-5 (64, m.s.), 40-8 (m.s.), 40-33 (m.s.), 40-62, 40-64, 40-71, 40-91, 40-95 (m.s.), 40-110, 40-112, 40-113, 40-115, 40-120, 41-1 (54, m.s.), 41-1 (103, m.s.), 41-36, 41-46, 41-48, 41-87, 41-93, 41-99 (m.s.), 41-103 (m.s.), 41-107 (m.s.), 41-123 (m.s.), 41-130, 41-131, 41-133 (m.s.), 41-139, 41-140, 41-160 (m.s.), 41-168
li	"	40-1 (119, m.s.), 40-119 (m.s.), 41-65, 41-167, 41-178
li?	"	41-90
mi?	"	41-60
mr	"	40-133 (m.s.), 41-97 (m.s.)
ms2	"	41-92 (m.s.), 41-98
ms5	"	41-99
ms6	"	41-100
ms8	"	41-84
ms9	"	41-101
msl0	"	41-102
msl1	"	40-31 (m.s.), 40-51 (m.s.), 41-1 (103), 41-103
msl2	"	41-104 (m.s.)
msl3	"	41-105

msl4	Co	41-106
msl7	"	41-32 (m.s.), 41-33
msl8	"	40-62, 41-107 (m.s.), 41-133 (m.s.)
ms37	"	41-109
msx	"	40-1 (74, m.s.), 40-5 (74, m.s.), 40-67, 40-68 (m.s.), 40-74, 41-95 (m.s.), 41-111 (m.s.), 41-120 (m.s.), 41-142
ms?	"	41-58 (m.s.), 41-140
Mt?	"	41-155, 41-178, 41-180
na	"	41-1 (54), 41-1 (182), 41-61, 41-182
na2	"	41-112
nl	"	40-30 (m.s.), 41-1 (113), 41-2 (113), 41-113, 41-114, 41-115 (m.s.)
nl2	"	40-2 (123, m.s.), 40-123 (m.s.), 41-1 (116), 41-116 (m.s.)
nl?	"	41-58
o	"	40-17, 40-42, 41-117
o2	"	40-128, 41-118, 41-146
Og	"	41-26, 41-65
pwr	"	40-1, 40-2, 40-3 (95), 40-5 (115), 40-5 (74), 40-5 (84, m.s.), 40-6 (84, m.s.), 40-5 (84, m.s.), 40-6 (84, m.s.), 40-7, 40-9, 40-10, 40-11, 40-12, 40-13, 40-14, 40-15, 40-16, 40-17, 40-19, 40-20, 40-21, 40-22, 40-23, 40-24, 40-25, 40-26, 40-27, 40-28, 40-29, 40-30, 40-31, 40-41, 40-48, 40-52, 40-53, 40-54, 40-55, 40-57, 40-62, 40-74, 40-81, 40-83, 40-84, 40-95, 40-108, 40-115, 40-118, 40-127, 40-128, 40-129, 41-1, 41-24, 41-28, 41-29, 41-49, 41-51, 41-52, 41-55, 41-62, 41-68, 41-75, 41-76, 41-77, 41-78, 41-89, 41-90, 41-92, 41-95, 41-97, 41-98, 41-102, 41-107, 41-111, 41-112, 41-115, 41-118, 41-124, 41-126, 41-133, 41-134, 41-140, 41-145, 41-146, 41-158, 41-159, 41-168, 41-174, 41-175, 41-184, 41-192
pcw	"	41-39, 41-142
pcr	"	41-142
PVV	"	40-15, 40-39, 40-125, 40-126, 41-16, 41-17, 41-32, 41-80, 41-176
P	"	40-1 (109, m.s.), 40-1 (71), 40-2 (71), 40-2 (123), 40-4 (65, m.s.), 40-8, 40-18, 40-33, 40-43, 40-51, 40-65, 40-71, 40-72, 40-76, 40-109, 40-123, 40-134, 41-1 (57), 41-7, 41-40, 41-41, 41-42, 41-46, 41-56, 41-87, 41-99, 41-100, 41-103, 41-109, 41-114, 41-116, 41-119, 41-137, 41-138, 41-154, 41-164, 41-169
P?	"	41-72
pb4	"	41-122
pbx	"	41-123 (m.s.), 41-124
pb?	"	40-67 (m.s.), 41-120
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J. E. Welch

MAIZE GENETICS COOPERATION

NEWS LETTER

17

1943

The data presented here are not to be used in
publications without the consent of the authors.

Department of Plant Breeding
Cornell University
Ithaca, N. Y.

MAIZE GENETICS COÖPERATION
DEPARTMENT OF PLANT BREEDING
CORNELL UNIVERSITY
ITHACA, NEW YORK

December 10, 1942

To Maize Genetics Cooperators:

This is the annual call for copy for the next News Letter. I have set January 31, 1943, as the deadline date for this material. Please send copy to the Department of Plant Breeding, Cornell University, where it will be assembled and forwarded to me at Pasadena, California.

Since the emergency has doubtless made it impossible for some of you to continue your genetic studies, those who have material suitable for the News Letter should make an effort to get it to me on time.

Sincerely,

RAEmerson

R. A. Emerson

RAE:P

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I. REPORTS FROM COÖPERATORS

The data presented here are not to be used in publications without the consent of the authors.

R. A. Emerson

Bureau of Plant Industry Station, Beltsville, Md.

Several backcross progenies involving genes located on chromosomes 3 and 7 were grown in 1941. They were not reported in the last News Letter as the data had not been summarized, hence they are reported now. A few additional backcross progenies were grown during the past season and are reported. Cold, wet weather following planting resulted in very poor stands in both seasons, but it is felt that the segregations obtained are not sufficiently distorted to modify gene order.

1. Backcrosses involving genes on chromosome 7.

		<u>gl</u>		<u>ij</u>	<u>bd7</u>				
		+		+	+				
0		1		2		1-2		Total	
69	53	4	4	68	26	4	2		
122		8		94		6		230	

Linear order and map distances are: gl - 6.1 - ij - 43.5 - bd7
(500 seeds were planted, 46.0% produced mature plants.)

		<u>gl</u>		<u>sl</u>	<u>ij</u>			
		+		+	+			
0		1		2		1-2		Total
268	182	32	52	2	5	0	2	
450		84		7		2		543

Linear order and map distances are: gl - 15.8 - sl - 1.7 - ij
(1,000 seeds planted, 54.3% produced mature plants.)

		<u>02</u>		<u>ra</u>	<u>gl</u>	<u>ij</u>										
		+		+	+	+										
<u>0</u>		<u>1</u>		<u>2</u>		<u>3</u>		<u>1-2</u>		<u>1-3</u>		<u>2-3</u>		<u>1-2-3</u>		<u>Total</u>
273	213	24	28	6	3	49	56	1	1	5	7	0	2	1	0	
486		52		9		105		2		12		2		1		669

Linear order and map distances are: 02 - 10.0 - ra - 2.1 - gl - 17.9 - ij
(1,000 seeds planted, 66.9% produced mature plants.)

		02		ij		bd7			
		+		+		+			
0		1		2		1-2		Total	
69	56	24	44	38	44	7	17		
125		68		82		24		299	

Linear order and map distances are: 02 - 30.8 - ij - 35.5 - bd7
(500 seeds were planted, 59.8% produced mature plants.)

2. Backcross involving lg2 and genes on Chromosome 3.

		rt		+		lg2		a	
		+		Rg		+		+	
0		1		2		3		1-2	
58	77	7	6	36	38	28	35	4	2
135		13		74		63		6	
								4	3
								15	11
								0	1
								1	
									325

Linear order and map distances are: rt - 8.3 - Rg - 32.9 - lg2 - 29.8 - a
(500 seeds planted, 63.0% produced mature plants.)

Merle T. Jenkins

California Institute of Technology, Pasadena, California

Much detailed information has been collected on the numerous translocations under study. I do not feel that this information would be of enough general interest to be reported in raw form in the News Letter. Some time I hope to get it organized in more useful form. Here are a few miscellaneous items, and a brief statement on the practical use of translocations.

1. A plant homozygous for Tl-2c but heterozygous for striate and pericarp color (repulsion) backcrossed gave +P28, +p49, sr P43, sr p25 showing linkage with about 37 per cent crossing over. Since Tl-2c is very close to sr, this places it to the left of sr, substantiating the indications from previous data submitted by Emerson and by myself.

2. A crossover has been obtained between Yl and T6-9b, which may help to determine the position of Yl on the chromosome. The position of Yl has been made difficult by the great amount of suppression of crossing-over which has characterized all translocations thus far studied in the proximal half of the long arm of chromosome 6.

3. A number of new translocations have been isolated and some information collected. They include the following which have been

identified as to chromosomes involved.

Index number	Chromosomes	Index number	Chromosomes
a-33	1-3	F-2	2-10
c-43	1-3	a-101	3-5
g-3	1-3	a-22	3-8
c-15	1-3	a-94	3-9
a-37	1-5	a-26	4-9
a-80	1-6	c-31	4-9
B-49	1-7	F-22	4-9
D-5	1-7	B-45	4-10
B-42	1-8	B-10	5-8
C-36	1-10	B-70	5-10
a-29	2-4	a-66	6-9
c-40	2-8	F-33	8-10

4. One complex translocation (Index No. B-2) involves four chromosomes 1, 3, 4, and 5. It is closely linked to su. It is also close to bm with much suppression of crossing-over between bm and pr. No linkage information has been obtained on chromosomes 1 and 3.

5. Utilization of translocations with endosperm markers in the study of economic traits. In studying the inheritance of any difficult trait, a simple test can be made for linkage with an endosperm character such as su or wx, especially if the multiple recessive combination occurs in one of the commercial inbred lines. For example, in studying resistance to bacterial wilt, a resistant line can be crossed with a susceptible sugary, and the F_1 crossed to a susceptible sugary inbred. Comparison can then be made between the resistance of plants from starchy vs. sugary seeds of the backcross ear. This tests for resistance genes in the central portion of chromosome 4. If this test is negative then a similar test can be made involving translocation 1-4a. (Resistant x su T1-4a) x susceptible sugary inbred. A test of plants from su vs. su seeds then becomes a test for resistance genes in the long arm of chromosome 1. From the standpoint of testing technique, it means that su can be used as a marker for any chromosome or part of a chromosome for which the proper translocation is available. And the same recessive sugary inbred line can be used for all backcrosses. The suppression of crossing-over in the neighborhood of the translocation aids in making the method more efficient in detecting linkages. If an appropriate series of translocations existed, it would be possible to cover the entire chromosome complement with the use of one endosperm gene such as su.

The series of translocations available at present is not sufficient to cover all chromosomes using only one marker gene. By using two series, one with su, the other with wx, it is possible to have at least one translocation for each chromosome. More translocations are being isolated and it is hoped that, year by year, the series available for this purpose will be greatly improved and simplified.

Work on the inheritance of economic traits by using endosperm marked translocations is being taken up at several of the corn belt experiment stations. To facilitate these programs I have made the F_1 crosses here at Pasadena with such translocations as are now available. These were:

su series - 1-4a, 2-4a, 2-4c, 4-5b, 4-5d, 4-6a, 4-8, 4-9a, 4-10b and a new 2-4 (a-29)

For sweet corn lines I was able to add 4-7a, a new 4-9 (F-22), 4-10 (B-45) and a multiple 1-3-4-5 (B-2)

wx series - 1-9a, 1-9c, 2-9b, 3-9a, 3-9b, 3-9c, 4-9b, 6-9a, 8-9a, 9-10b and new 4-9 (F-22), and 6-9 (a-66)

pr series - 1-5a, 1-5c, 2-5b, 3-5b, 3-5c, 4-5c, and 4-5d

The above is too large a series for completion of tests, except for such traits as can easily be tested in the seedling stage. But the additional F_1 's may serve as a reserve for checking any indications of linkage.

6. Use of translocations in corn breeding. Once any significant gene for an economic trait is located, it should be possible to transfer that gene to any commercial inbred line with only a minimum of alteration of the inbred line itself. In simplest form, the inbred line would first be crossed with the proper translocation (one near the locus of the gene). The F_1 would then be backcrossed recurrently to the inbred line selecting always the semisterile plants. Then on selfing, the homozygous translocation inbred can be isolated. The next step consists of crossing the translocation inbred with the desired gene, and backcrossing to the translocation inbred. Then, on selfing and eliminating the translocation, the result should be essentially the inbred line homozygous for the desired gene. The length of time required is considerable, but can be reduced by various shortcuts. No great number of plants need be grown, nor is much labor required. And an economic gene could be transferred to any number of inbred lines simultaneously. This method is suggested only for such traits as are difficult to follow, such as for example resistance to disease, insects, drouth or cold. It is essentially an indirect method which controls the valuable but difficult character by substitution of pollen semisterility which can be easily and precisely followed.

E. G. Anderson

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1. Relation between knobs and chromocenters of interkinetic nuclei. - Resting nuclei of maize stained with Feulgen contain discrete, deeply-staining bodies in addition to diffuse chromatic material. These deeply-staining bodies are called chromocenters. A good correlation was found between the number of chromocenters in the interkinetic nuclei and the

number of knobs present in the pachytene chromosomes. In strains free from conspicuous knobs but possessing B chromosomes a good correlation was found between the number of B chromosomes and the number of chromocenters. The chromocenters derived from B chromosomes are not as large as those from some of the larger knobs -- evidently all of the heteropycnotic material observed in the B chromosomes at pachytene is not represented in the chromocenter. That portion of the B chromosome immediately adjacent to the centromere of the B is more knob-like in appearance than other portions of the chromosome and it is believed that it is this proximal portion which forms the chromocenter. Plants free from conspicuous knobs and B chromosomes have a great majority of their interkinetic nuclei free from any structures which might be interpreted as chromocenters (except for the two nucleolar organizer regions on chromosome 6). That chromocenters often fuse is indicated by the range in number and size. Strains with knobs of approximately uniform size have chromocenters of uniform size -- barring fusion - while strains with different sized knobs have a marked range in size of chromocenters. The data obtained are summarized in the following table.

Tissue studied	Strain	Knob No. at pachytene	B chrom. No.	Number nuclei counted	Mean No. chromocenters	Range in number	Modal class
root	A	9	0	100	8.16	4-11	8
style	A	9	0	100	8.00	4-12	8
root	B	6	0	100	5.05	2-8	5
root	C	6	0	100	5.22	2-6	5
root	D	0	4	100	3.27	1-5	4
root	E	0	0	100	0.22	0-1	0

Occasionally the number of bodies classified as chromocenters was greater than the number of conspicuous knobs. This may be due to the misclassification of diffuse heterochromatin as chromocenters or more likely to the failure to distinguish small knobs at pachytene. Fusion of two or more of these small knobs might give rise to recognizable chromocenters. In every strain studied the number of chromocenters was determined before that of knob number. All preparations were stained with the Feulgen reaction.

D. T. Morgan, Jr.

2. The interaction of bronze (bz) with factors determining anthocyanin colors. - The bronze (bz) gene modifies the pigments involved in plant color. A B Pl bz plants are not purple but are a deep reddish-brown. A B pl bz plants have a bronze instead of a sun red color - the bronze color is also a sun color. A b Pl bz and A b pl bz plants are pigmented but the normal red pigment of the culm and glumes is transformed into a brownish pigment. The bronze gene is not concerned with the primary reactions determining the presence or absence of color but does modify in some way the pigment molecule. Aleurone color is also affected by bronze - the effect being a 'bronzing' of the purple (Pr) and red (pr) pigments. Pericarp

color is not affected i.e. plants of A P bz constitution have red pericarp. The action of bz on both the plant and aleurone colors may indicate a close chemical relationship of these pigments. The following linkage data on the location of bz have been obtained:

	Percent recombination	Number of individuals
<u>Yg2-Bz</u> self	13	2656
<u>Bz-C</u> B.C.	5	573
<u>Bz-C</u> self	5	3135
<u>Bz-Sh</u> self	8	454
<u>Bz-Sh</u> self	10	739
<u>Bz-Wx</u> self	24	454
<u>Bz-Wx</u> self	30	739
<u>Bz-V</u> self	33	739

On the basis of the above data, which are mostly F_2 , the bz gene falls between yg2 and C. Inasmuch as Dt is 7 units beyond yg2 the revised linkage map of chromosome 9 is tentatively as follows:

<u>Dt</u>	<u>Yg2</u>	<u>Bz</u>	<u>C</u>	<u>Sh</u>	<u>Bp</u>	<u>Wx</u>	<u>V</u>
0	7	21	26	29	44	59	71

3. Gametophyte factor in chromosome 3. A gamete factor having an adverse effect upon the ability of pollen grains possessing it to effect fertilization has been located in chromosome 3. This new gamete factor is independent of the genetic constitution of the silks and hence is different in this respect from the gamete factors in chromosomes 4 and 5. Pollen with this factor is not visibly different from normal. Approximately 12.7% of the functioning pollen from heterozygous plants carry the gamete factor. The linear order in chromosome 3 is Lg2 A ga with the gamete locus some 10-12 units from A. Presumably it should lie close to etched (et).

4. The preference of Jap beetles for liguleless-1 leaves. The severe infestation of Japanese beetles in the summer of 1942 at Irvington, N. Y. made possible the observation that these beetles found the leaf tissue of liguleless-1 (lg1) plants very much to their liking. Leaves of all lg tester strains were nearly destroyed and many plants died. In all cultures segregating for lg1 an accurate classification for lg and Lg could be made from the amount of leaf tissue eaten by the insects. Lg plants adjacent to sister lg plants were nearly free from beetles while the lg plants literally swarmed with them. Plants homozygous for lg2 had the same, or nearly so at any rate, degree of infestation as did their normal sibs.

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1. A late flowering mutation arising in one of the long inbred Leaming strains, Cl4, shows no appreciable differences in plant or seed size at full maturity. At two weeks after planting the late plants are about half as tall as the normal inbred plants. These slower-growing plants are about six days later in silking but continue rapid growth longer and finally arrive at approximately the same height at the end of the season. This is an example of a deleterious recessive, not easily detected, that slows physiological activity.

2. Reciprocal crosses between inbred strains may show small differences in amount of growth in early stages after germination due to differences in embryo size or seed condition. These differences usually disappear by the time the plants flower. In crosses of a Rice pop inbred with very small seeds and a yellow dent inbred with large seeds marked differences were obtained in the reciprocals. Three weeks after planting the dent parent was nearly twice as tall as the pop parent and proportionally larger in overall size dimensions. At this stage the dent x pop F_1 is taller than the dent parent while the pop x dent F_1 occupies an intermediate position between the two parents. The hybrids and parents tassel and silk in the same order as their initial embryo weights: (1) dent x pop, (2) dent parent, (3) pop x dent, (4) pop parent. At the end of the season the two reciprocal crosses are equal in production of grain and in height and both are taller and more productive than either parent. Production of grain of the hybrid is about 15 times that of the pop parent and nearly twice as much as the dent. Both reciprocals reach full maturity at about the same time but the one that is smaller at the start continues rapid growth longer to reach eventually the same height and production of grain in approximately the same length of time. Since one of the hybrids starts smaller after germination and ends up larger in the amount of material produced than the larger parent, in the same period of growth, one is growing at a faster rate than the other.

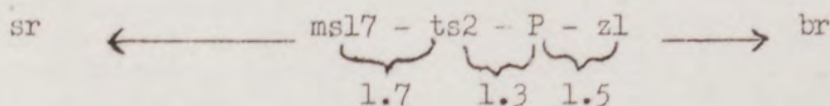
The parents and reciprocal crosses also differ in the number of tillers. The dent inbred averages .03, dent x pop 2.06, pop x dent 1.24, and pop inbred 2.83 tillers per plant. The larger number of tillers is shown by the hybrid with the non-tillering seed parent. In these reciprocal crosses having the same genic constitution, tillering is an expression of initial vigor large enough to overcome any differences in maternal effect. Differences that may exist in the cytoplasm of these two widely diverse reciprocal crosses have no effect on the final reaction product between the external environment and the nuclear construction of the hybrids.

D. F. Jones

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1. Aberrant pericarp-color ratios. - A few years ago I reported a recessive zygotic lethal, z1, with its locus near P in chromosome 1 of maize (Genetics 24: 368-384. 1939). The effect of z1 is to prevent,

with rare exceptions, homozygosis of genes with which it is closely linked, and thereby to change a 3:1 to a 2:1 F_2 ratio when zl is linked with a dominant gene or to prevent the occurrence of one class when linked with a recessive gene. When a plant heterozygous for zl is crossed with one lacking zl, there is, of course, no disturbance of ratios in the resulting progeny. The locus of zl, relative to other chromosome-1 genes is



Another case of disturbed pericarp-color ratios has occurred in at least three supposedly unrelated lines, all of which, however, are found to have had one individual plant as a common ancestor a few generations back, namely, a chromosome-1 marker with the genotype P br an gs. This suggests that the disturbance is associated with P rather than with its recessive allele.

Two selfed red-eared plants gave progenies totaling 83 red to 89 white, while three other selfed reds gave progenies with normal 3:1 ratios. The former also gave aberrant and the latter normal ratios when used as the pollen parent in crosses with white-eared plants. Fourteen cultures, resulting from white pollinated by heterozygous red, have had a total of 329 plants with red and 1148 with non-red ears. Some of these crosses have involved also T1-3a, the totals being 404 T and 120 non-T. Two cultures involved msl7, P, and T1-3a, from the cross:

$\text{ms} + + \times \frac{+ \text{P} +}{\text{ms} + \text{T}}$. This 3-point test gave the following results:

0	1	2	1,2	Total
18 152	0 6	10 18	0 2	
170	6	28	2	206
	2.9%	13.6%	1.0%	

The percent of recombination is: ms - P = 3.9, P - T = 14.6. The recombination value for P - T is less than that indicated by Anderson (News Letter 14 p.2. 1940). The striking thing, however, is the ratios of dominant to recessive markers, as follows:

$$\begin{array}{l} + : \text{ms} = 28 : 178 \\ \text{P} : + = 36 : 170 \\ + : \text{T} = 42 : 164 \end{array}$$

From these aberrant ratios it may be inferred that the locus of the disturbing element is to the left of msl7. Whether the disturbing factor is transmitted through the egg is not known. It is transmitted through the pollen. Only a part of the red ears of a culture that shows the aberrant ratio yield such ratios in the following generation.

The nature of the responsible gene, if gene it is, is not known. It is certain, however, that it is not a recessive zygotic lethal and not a

complete pollen lethal. So far as now known, it might be a pollen semi-lethal or a gamete factor, but if the latter, it differs in some respects from the Ga gene that disturbs the ratios of the starchy-sugary pair and other characters of chromosome 4.

2. White-capped red pericarp. - In last year's News Letter I presented data which I interpreted as showing that white-capped red pericarp of such varieties of maize as Bloody Butcher is not allelic to ordinary red pericarp, P, as had been supposed, but is conditioned by multiple genes at least one of which is linked with red cob color and therefore with P. I presented data from F_2 , F_3 , and backcrosses of the cross of colorless pericarp and white cob, W-W, with white-capped pericarp and red cob, C-R. From this cross, the four possible combinations of pericarp and cob colors were obtained, namely, C-R, C-W, W-R, W-W. Grades of pericarp color from 0, no color, to 6, the color intensity of the Bloody Butcher parent, were reported and the behavior in inheritance was shown to be that typical of quantitative characters.

This year I present data from further F_3 cultures and also from F_4 cultures. For brevity in the accompanying table, I have grouped together cultures which have about the same ranges of variation, and may, therefore, in so doing, have combined genetically heterogeneous material.

Certain conclusions may be drawn from these data: (1) - From the cross W-W x C-R, there have appeared in F_3 or F_4 in relatively true breeding form, the four possible combinations of pericarp and cob colors, namely, W-W (item 1), W-R (item 2), C-W (items 21, 28), and C-R (items 20, 25, 29, 30, 33). (2) - There have appeared types that breed relatively true for pericarp color while still segregating for cob color: W-R and W-W (item 3), C-R and C-W (items 22, 26, 27). (3) - Some cultures still show marked variation in intensity of pericarp color while breeding true for red cobs (items 11, 17) or white cobs (items 10, 16). (4) - In all cultures that have any pericarp color and that are segregating for cob color, the ears with red cobs have a higher mean grade of pericarp color than do those with white cobs. (5) - In a few cases, the ears with white cobs have no pericarp color while some or all of those with red cobs have more or less pericarp color (items 5, 6, 7, 18). (6) The gene or genes conditioning pericarp color in these instances (5 and 6 above) may be assumed to be in chromosome 1 near the locus of P. (7) - Selection is effective in establishing lines with diverse intensities of pericarp color.

From the trisomic cultures of Mr. Einset has come the suggestion that one or more genes affecting white-capped red pericarp color may be in chromosome 5. In a culture segregating for trisome 5 and for this type of pericarp color, the ears of trisomic plants had unmistakably more intense pericarp color than did those of disomic ones. This behavior is to be expected of characters that show a gene-dosage effect as white-capped pericarp color does. A beginning has been made in the use of the other trisomes in an attempt at a further genetic analysis of this pericarp color.

3. Differential dominance in number of kernel rows. - In the 1940 News Letter (14: 19-21), I reported differences in relative dominance of ten inbred lines of 12-row maize and of two 8-row inbred lines in crosses

F₃ and F₄ cultures of the cross W-W x C-R

: Number : Grade :				Progenies									
Item:	of	of	Cob :	Pericarp-color grades						:	Mean		
No.:	cultures:	parent:	color:	0	1	2	3	4	5	6:	Total:	grade	
1 :	3 :	0 :	W :	134	-	-	-	-	-	-:	134 :	0	
2 :	2 :	0 :	R :	116	-	-	-	-	-	-:	116 :	0	
3 :	2 :	0 :	{R :	73	-	-	-	-	-	-:	73 :	0	
			{W :	25	-	-	-	-	-	-:	25 :	0	
4 :	1 :	0 :	R :	51	4	-	-	-	-	-:	55 :	0.1	
5 :	1 :	0 :	{R :	32	6	-	-	-	-	-:	38 :	0.2	
			{W :	15	-	-	-	-	-	-:	15 :	0	
6 :	1 :	1 :	{R :	2	10	-	-	-	-	-:	12 :	0.8	
			{W :	6	-	-	-	-	-	-:	6 :	0	
7 :	1 :	1 :	{R :	13	19	6	1	-	-	-:	39 :	0.9	
			{W :	8	-	-	-	-	-	-:	8 :	0	
8 :	1 :	2 :	W :	6	8	16	12	-	-	-:	42 :	1.8	
9 :	1 :	2 :	{R :	9	5	12	10	-	-	-:	36 :	1.6	
			{W :	4	2	2	3	-	-	-:	11 :	1.4	
10 :	8 :	3 :	W :	56	36	46	66	17	-	-:	221 :	1.8	
11 :	1 :	3 :	R :	2	1	2	3	13	5	-:	26 :	3.5	
12 :	2 :	3 :	{R :	8	1	7	23	10	-	-:	49 :	2.5	
			{W :	9	2	3	6	2	-	-:	22 :	1.5	
13 :	3 :	3 :	W :	-	14	17	29	8	-	-:	68 :	2.5	
14 :	1 :	3 :	R :	-	6	16	13	11	-	-:	46 :	2.6	
15 :	1 :	3 :	R :	-	-	-	6	5	-	-:	11 :	3.5	
16 :	1 :	4 :	W :	14	3	8	11	19	5	-:	60 :	2.6	
17 :	2 :	4 :	R :	13	20	12	25	12	3	-:	85 :	2.1	
18 :	1 :	4 :	{R :	-	6	4	10	4	-	-:	24 :	2.5	
			{W :	10	-	-	-	-	-	-:	10 :	0	
19 :	2 :	4 :	R :	-	6	9	19	29	9	-:	67 :	3.6	
20 :	1 :	4 :	R :	-	-	3	21	12	1	-:	37 :	3.3	
21 :	4 :	4 :	W :	-	-	7	76	70	2	-:	155 :	3.4	
22 :	2 :	4 :	{R :	-	-	-	10	49	10	-:	69 :	4.0	
			{W :	-	-	4	13	6	-	-:	23 :	3.1	
23 :	2 :	5 :	{R :	9	7	4	16	17	21	1:	75 :	3.2	
			{W :	7	2	4	8	2	-	-:	23 :	1.8	
24 :	1 :	5 :	R :	-	2	8	9	16	8	-:	43 :	3.5	
25 :	1 :	5 :	R :	-	-	2	3	7	6	-:	18 :	3.9	
26 :	1 :	5 :	{R :	-	-	1	10	12	9	-:	32 :	3.9	
			{W :	-	-	3	6	-	-	-:	9 :	2.7	
27 :	1 :	5 :	{R :	-	-	-	1	8	16	-:	25 :	4.6	
			{W :	-	-	-	-	4	2	-:	6 :	4.3	
28 :	1 :	5 :	W :	-	-	-	3	12	5	-:	20 :	4.1	
29 :	3 :	5 :	R :	-	-	-	12	34	73	7:	126 :	4.6	
30 :	2 :	5 :	R :	-	-	-	-	25	55	1:	81 :	4.7	
31 :	1 :	6 :	{R :	-	-	-	2	14	15	3:	34 :	4.6	
			{W :	-	1	2	6	-	-	-:	9 :	2.6	
32 :	1 :	6 :	R :	-	-	1	3	9	34	12:	59 :	4.9	
33 :	2 :	6 :	R :	-	-	-	-	12	42	33:	87 :	5.2	

of 12-row with 8-row lines. I now present further data on the crosses previously reported and tests of a few inbred lines not represented in the earlier report. The accompanying table includes the earlier as well as the later data.

Number of individuals and mean row number of F₁ crosses
of 8-row with 12-row inbreds

12-row:	8-row lines					
lines :	1	:	51	:	Snf. W : Y. Flr.:	Y. Flt. : R. Flt.
VI :	60- 8.9	:	54- 9.7	:	:	:
IV :	178- 9.1	:	72- 9.6	:	:	:
III :	75- 9.0	:	164-10.1	:	:	:
VII :	120- 9.2	:	91-10.1	:	:	194- 9.3 :
2 :	346- 8.9	:	391-10.5	:	103-8.8 : 79-8.8	114- 9.5 : 62-9.9
II :	89- 9.7	:	129-10.1	:	:	:
4 :	258- 9.4	:	177-10.6	:	:	:
39 :	625- 9.6	:	716-11.4	:	:	213- 9.7 :
G :	93- 9.1	:	37-10.1	:	137-8.6 :	217- 9.4 :
B :	221- 9.1	:	284-10.5	:	144-9.0 :	151- 9.7 : 81-9.5
b :	80- 9.8	:	58-10.4	:	78-9.2 : 87-9.4	:
c :	91-10.5	:	88-11.1	:	76-9.6 :	81-10.3 :

Averages of comparable means

:	9.4	:	10.4	:	:	:	:
:	9.5	:	10.5	:	9.0	:	:
:	9.4	:	10.5	:	:	9.1	:
:	9.4	:	10.6	:	:	:	9.7
:	9.0	:	10.5	:	:	:	9.7

Key to line designations:

1. Luce's Favorite (Wiggans)	VII. Early Pride
2. Onondaga White (Wiggans)	R. Flt. Red Flint
4. Bloody Butcher (Wiggans)	Snf. W. Sanford White
39. Golden Bantam (Purdue)	Y. Flr. Yellow Flour
51. Golden Bantam (Purdue)	Y. Flt. Yellow Flint
II. Westbranch	B } Segregates from crosses G } of 8-row with 16-row b } lines c }
III. Queen's Golden	
IV. White Pop	
VI. Dutton's Flint	

Of the 8-row inbreds, Sanford White and Yellow Flour are somewhat more nearly dominant even than Luce's Favorite, while Yellow Flint and Red Flint are less nearly recessive than Golden Bantam. Similar differences are shown by different 12-row lines. Such differences are well illustrated by the following frequency distributions for number

of kernel rows in crosses of two 12-row with two 8-row lines:-

<u>Cross</u>	<u>8</u>	<u>10</u>	<u>12</u>	<u>14</u>	<u>Total</u>	<u>Mean</u>
1 with 2	199	144	3		346	8.9
1 " 39	151	437	37		625	9.6
51 " 2	61	183	145	2	391	10.5
51 " 39	13	196	497	10	716	11.4

That these differences in behavior are conditioned by gene differences rather than by cytoplasmic diversity is indicated by the fact that reciprocal crosses are essentially alike. The following data from reciprocal crosses are all that are now available:

<u>Cross</u>	<u>8</u>	<u>10</u>	<u>12</u>	<u>14</u>	<u>Total</u>	<u>Mean</u>
2 x 1	69	58	2		129	9.0
1 x 2	79	55	1		135	8.8
39 x 1	65	227	19		311	9.7
1 x 39	70	187	10		267	9.6
39 x 51	9	135	371	5	520	11.4
51 x 39	3	32	67	3	105	11.3

It is not surprising that 12-row lines exhibit differences in relative dominance, because several of them at least are known to have different row-number genotypes. But 8-row types have been assumed to have the same genotype for number of kernel rows. Negative evidence in support of this notion is: (1) Crosses of 8-row inbreds have not resulted, in my experience, in the production of other than 8-row types. (2) Crosses of 8-row with 12-row inbreds have not resulted in types with more than 12 kernel rows. It is, of course, conceivable that genes responsible for the 8-row condition may be alleles with the same effect on row number but with somewhat different dominance behavior.

4. Genetic diversity of 12-row lines. - Data indicating genetic heterogeneity of certain 12-row inbred lines of maize have long been available, but have not been reported heretofore in this "unpublished publication". A brief summary of some of these data follow.

Numerous 12-row lines have been obtained from various sources. Some (A, B, G, b, c) from crosses of 8-row flints with 16-row dents and others (III, IV, VI, VII) by selection from varieties of dent, flint, and popcorn. No 12-row type produces only 12-row ears. There are always some 10-row and 14-row ears and occasionally an 8-row or a 16-row ear. To determine whether a 12-row line is homozygous it is necessary to grow progenies from selfed ears of the more extreme variants. To get such selfed ears it is necessary to hand-pollinate many plants. This has been accomplished for the 12-row types involved in this account. A single example of the results obtained is given here.

Line b had in F₉ a distribution ranging from 8 to 16 rows with

frequencies of 4-18-49-14-1. In F_{10} , progenies from selfed ears of diverse row numbers were produced as follows:

Parent row number	Progeny					<u>Total</u>	<u>Mean</u>
	<u>8</u>	<u>10</u>	<u>12</u>	<u>14</u>	<u>16</u>		
8		1	19	7	1	28	12.6
10		5	22	9		36	12.2
12	2	3	27	6	2	40	12.2
14		4	25	3	2	34	12.2
16	4	4	34	9	1	52	12.0

The other lines gave similar results. It was concluded, therefore, that all were approximately homozygous. When any two of the nine 12-row lines were crossed, except only b x c, it was easily possible to establish lines of different row number. For example, the cross b x IV exhibited row-number ranges from 10 to 16 in F_1 and 8 to 18 in F_2 with these frequencies, respectively, 1-43-8-1 and 2-12-37-21-7-2. In F_3 the following frequency distributions were observed:

Parent row number	Progeny						<u>Total</u>	<u>Mean</u>
	<u>8</u>	<u>10</u>	<u>12</u>	<u>14</u>	<u>16</u>	<u>18</u>		
8	34	12	2				48	8.7
10	2	1	33	7	2		45	12.3
14			6	16	14	1	37	14.5

Given different genes for row number in the several 12-row types, it should be possible, by multiple crossing followed by selection, to assemble the row-number genes of the several 12-row lines into a single line of high row number. In the accompanying table are shown the frequency distributions of all of the ears produced by seven inbred lines during several generations when selected for twelve rows and similar data from certain single, double, and multiple crosses of these lines when selected for high row number.

The seven inbred lines had frequency distributions ranging mostly from 8 to 16 rows with strong modes at 12 rows and means very near 12. During the five to eight generations shown in the table and among the total of more than six thousand ears, not a single ear had more than 16 rows. After repeated intermittant crossing followed by selfing with selection for high row number, lines have finally been established with modes at 24 rows and means near 23. Two of these lines have not produced an ear with so few as 16 rows.

Frequency distributions of number of kernel rows of inbred lines
and their single, double, and multiple crosses

Inbred lines and crosses	Gener- ations: (F)	Number of kernel rows											Total	Mean
		8	10	12	14	16	18	20	22	24	26	28		
A	5-9	8	303	680	147	3	-	-	-	-	-	-	1141	11.7
B	5-12	19	594	1267	411	1	-	-	-	-	-	-	2292	11.8
G	3-13	2	107	701	500	27	-	-	-	-	-	-	1337	12.7
III	3-8	2	39	242	55	6	-	-	-	-	-	-	344	12.1
IV	3-10	8	65	305	47	-	-	-	-	-	-	-	425	11.8
VI	4-10	5	126	406	144	3	-	-	-	-	-	-	684	12.0
VII	3-9	-	55	284	81	4	-	-	-	-	-	-	424	12.2
A x B	4-5	-	8	74	95	10	-	-	-	-	-	-	187	13.1
A x G	4-5	-	-	50	136	52	1	-	-	-	-	-	234	14.0
IV x VI	4-5	-	1	51	108	42	5	-	-	-	-	-	207	14.0
VI x VII	5-6	-	-	43	109	73	9	-	-	-	-	-	234	14.4
III x IV	5-6	-	-	38	105	62	16	-	-	-	-	-	221	14.5
IV x VII	5-6	-	-	14	98	120	14	-	-	-	-	-	246	15.0
A-B x VI-VII	5	-	-	7	7	36	17	5	-	-	-	-	72	16.2
A-B x IV-VI	5	-	-	1	7	37	14	6	-	-	-	-	65	16.5
A-B x III-IV	3-5	-	-	1	7	30	33	2	-	-	-	-	73	16.8
A-G x VI-VII	5	-	-	4	9	35	30	12	-	-	-	-	90	16.8
A-G x IV-VII	5	-	-	-	5	17	42	17	1	-	-	-	82	17.8
III-IV x IV-VII	5	-	-	-	-	22	29	15	-	-	-	-	66	17.8
III-IV x VI-VII	5	-	-	-	5	24	24	21	2	-	-	-	76	17.8
A-B x III-IV	1	-	-	-	-	3	1	-	-	-	-	-	4	
A-B x VI-VII														
A-G x IV-VII	1	-	-	-	5	22	18	3	-	-	-	-	48	16.8
III-IV x VI-VII														
A-G x VI-VII	1	-	-	-	-	11	19	12	3	-	-	-	45	18.3
III-IV x IV-VII														
A-B x III-IV	4	{	-	-	-	7	24	36	15	8	-	-	90	19.8
A-B x VI-VII			-	-	-	3	19	28	19	10	1	-	80	20.4
x			-	-	-	2	8	18	14	5	-	-	49	20.6
A-G x IV-VII			-	-	-	-	-	-	-	-	-	-		
III-IV x VI-VII														
A-B x III-IV	4	{	-	-	-	1	2	12	13	20	9	4	61	23.0
A-B x VI-VII			-	-	-	-	3	20	18	27	6	1	75	22.4
x			-	-	-	-	7	12	27	32	16	4	98	23.0
A-G x VI-VII			-	-	-	-	-	-	-	-	-	-		
III-IV x IV-VII														

I am now ready to admit that number of kernel rows in maize is a much more complex quantitative character than I assumed it to be when I began a study of its inheritance.

R. A. Emerson

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Controlling starchy contaminations in sweet corn by the use of Ga. - The gene Ga converged on Purdue 51 gives inbreds whose hybrids ("sixty-three sixty-fourths" Golden Cross Bantam) are resistant to pollen contaminations by field corn. In testing it was not found practicable to duplicate field conditions since the inclusion of "unadulterated" Golden Cross Bantam as a check, diluted the proportion of available Ga pollen.

Where this dilution was greatest, with four check rows to one row with Ga, Ga reduced contaminations by $71.6 \pm 20.4\%$ (S.E.). Where the proportion of Ga pollen was higher, the reduction was $76.6 \pm 11.8\%$. When the proportion was still higher (approaching field conditions) the reduction was $82.0 \pm 12.3\%$. Since the differences between these values are not significant, one can only guess that if Ga were introduced into both parents of the hybrid thus doubling the proportion of Ga pollen, Ga might under field conditions reduce contaminations by as much as 90%.

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Translocation 3-5d. - T 3-5d was isolated in an early dent corn from northern Wisconsin in 1938. (Shuman, John R., A chromosomal interchange in maize giving both chain and ring configurations and low sterility. Summaries of Doctoral Dissertations, University of Wisconsin Press 4: 57-58. 1940.) The strain was not subjected to any treatments known to induce chromosomal changes.

Interchange configurations at diakinesis were examined in 239 microsporocytes from a heterozygous plant, and 225 were classified as follows: 90.6% of the cells had chains of four chromosomes; 4.4% had four chromosomes in an open ring, 3.2% had closed rings of four chromosomes and 1.8% had 10 "bivalents". These observations were interpreted as evidence of a reciprocal translocation in which a comparatively short segment had been exchanged with a longer non-homologous one.

At Anaphase I, 79 microsporocytes from a heterozygous plant had an alternate disjunction of the chromosomes of the complex, and 97 showed an adjacent separation. These frequencies do not differ significantly from equality.

Diakinesis figures from hybrids combining the interchange under investigation with T 1-2a, T 2-9b, T 4-9a, T 6-8 had two independent complexes of four chromosomes and six bivalents; with T 3-8a and T 5-7a there was one complex of six chromosomes and seven bivalents; and with T 3-5b there was one complex of four chromosomes and eight bivalents. Hence chromosomes 3 and 5 were involved in the interchange; and it was labeled d since three T 3-5's were previously described.

Three plants heterozygous for T 3-5d had 24.4% of 2274 pollen grains aborted, and 26.8% of 1315 possible kernels missing from the corresponding ears. These two percentages do not differ significantly from each other, nor from the assumed 25% abortion.

Normal plants as the seed parent crossed with T 3-5d heterozygous resulted in 47.2% of 182 plants from two families with 25% pollen abortion. This per cent of partially sterile plants does not differ significantly from 50%, i.e. a 1 (normal) : 1 (25% sterile) plant ratio. T 3-5d heterozygous as the seed parent crossed with normal plants gave 37.4% of 251 plants from two families with 25% abortion. T 3-5d heterozygous plants sired produced 37.7% of 212 plants from two families with 25% abortion. Neither of the latter two distributions differ significantly from each other or from 33 1/3%, i.e. a 2 ("normal") : 1 (25% sterile) plant ratio.

It was therefore postulated that of the four equally frequent classes of spores expected in the heterozygote, only that class deficient for the longer interchanged segment is aborted. The class of spores deficient for the shorter segment but duplicate for the longer one survived through the seed - but not through the pollen parent - despite the fact that 75% of the pollen grains appeared normal. Normal plants, those heterozygous and homozygous for the interchange were morphologically indistinguishable. Plants homozygous for the translocation were completely fertile.

John R. Shuman

Missouri Botanical Garden

1. Maize from Michoacan. - Professor Ralph Beals of the University of California in making a detailed ethnographic study of two neighboring Tarascan villages in Michoacan, Mexico, collected 43 varieties of maize which were loaned me for study. There were 55 ears in all, from each of which I grew ten or more plants at the Blandy Experimental Farm during 1942. The ears were photographed, herbarium specimens were made of the leaves and tassels, measurements and notes were made on the living plants, and these data in condensed tabular form will eventually appear as an appendix to Professor Beals' monograph.

As a whole, the maize belongs to the race which Cutler and I have recently termed "Mexican Pyramidal". The ears taper sharply and regularly, most of them show more or less denting, and there is a strong but variable tendency to irregular rows. The plants are coarse

but the leaves break readily in the wind. They are very susceptible to smut. The tassels have few branches or none at all. At least three sub-races are grown in these two neighboring villages. For two of these there was enough material to define the central core of their variation. BLACK MAIZE is grown only below 8500 feet in gardens close to the homes. Characteristically it has large smoothly-dented kernels with blue or purple aleurone, on a tapering ear about 15cm. long. TULUKENIO varieties are grown only above 8500 feet in small isolated plots in the mountains. In size the ears vary from as large as Black Maize to very small nubbins. Their kernels vary greatly in size and shape but tend to be small, more or less pointed, and slightly dented. While a few have colorless seedcoats, most of them are lightly suffused or stained with red or reddish brown. None of them have dark aleurone. In such technical tassel characters as glume length, tassel branch number, and percentage of condensed internodes, the Tulukenio varieties are closer to Pima-Papago maize than to Mexican Pyramidal. The extreme variants of Tulukenio are small-cobbed, non-tapering, early seasoned, flinty, undented, and many tillered. They may possibly reflect a primitive small-cobbed race something like the maize of the prehistoric Basket Makers. Taken in conjunction with Mangelsdorf and Cameron's recent analysis of knob number in Guatemalan maize, the differences between the Tulukenio and the Black Maize varieties from the same village demonstrate the importance of considering altitude above sea level in interpreting the history and development of Zea mays.

Of the three Tulukenio varieties which were examined cytologically, two had 'B' chromosomes and the total knob numbers were 4, 4, and 7. The two Black Maize varieties which we examined had no 'B' chromosomes and had total knob numbers of 5 and 6. Most of the knobs were small, compared to those in the maize from western Mexico (Jalisco).

2. Glume bar and its inheritance. - Many central American and southwestern varieties of maize are characterized by a bar or spot of intense color at the base of the glume in the tassel. It is rather rare in modern dent corn; of eighty inbreds examined at Beltsville, 69 were without any indication of it and in only four was it strongly developed. In certain lines and under certain conditions it segregates sharply. It is apparently independent of both the B and R series though its expression is affected by them. It is easiest to score when the tassel has just emerged. I have used the following grades in scoring it:

readily apparent without handling the tassel	++
readily apparent only upon handling the tassel ...	+
of slight and variable expression	±
altogether lacking	0

The only data I have on its inheritance are derived from a series of inbreds from one strain of Papago Flour corn. In two cases the same lot of seed was grown in different places and different years. One second generation inbred was scored as all ++ at Cold Spring Harbor, L.I.; in 1941 and likewise at Boyce, Virginia in 1942. On the other hand the first generation inbred P-3 segregated sharply in Missouri in 1940, 10 ++ to 26 0. At Cold Spring Harbor in 1941 the second

planting gave a higher percentage of plants with glume bar but in many of these it was not strongly marked (43,+; 5,±; and 17, 0). In three of the inbreds glume bar segregated independently from the B and R loci. (Since the B and R allelomorphs in this material are apparently different from those in most genetic stocks, no attempt has been made to define them precisely).

P-2. leaf sheath slightly sun red, anthers pink, glume bar +. First selfing, 29 plants all sun red but in varying degree, anther color and glume bar segregating as follows: pink anthers,+, 11; pink anthers, 0, 11; green anthers,+, 4; green anthers 0, 1.

P-6. leaf sheath green, bright pink anthers, glume bar ++. First selfing, 27 plants segregating sharply for glume bar and plant color as follows: red sheath, ++5; green sheath, ++, 13; red sheath, 0, 3; green sheath, 0, 6.

P-8. parental type unscored. First selfing, 66 plants all strongly sun red, silks green, segregating for glume bar and anther color, red anthers,+, 37; green anther,+, 15; red anthers, 0, 7; green anthers, 0, 7.

3. Average values for certain characters in Beals' collections from Cherán and Nahuatzen (Uruapan) Michoacan, Mexico.

	Black Maize	Tulukenio
Total number of ears	25	26
Row number (from collected ears)	14	14
Glume length in mm.	13	12
Tassel branch number	5	7
Percentage of condensed internodes in tassel	10	20
Percentage of sub-sessile upper spikelets	50	70
Pubescence of sheath	scattered	heavy
Tillers on ten plants	0	0-1

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1. Some Alleles of R. Detailed phenotypic comparisons were made between R alleles derived from relatively unrelated individual plants. The original stocks were mostly of strains cultivated by various American Indian tribes, specimens of which were supplied by J. H. Kempton. Twenty-two alleles with colored aleurone and colored plant effects (R^r series) were included (abstract in Genetics, 28: 90-91). In addition a number of alleles of the r^r series are included in a

later parallel study.

The effect of different R alleles upon plant color differs widely, as to both intensity and distribution of pigmentation. Since the associated independent effect upon aleurone color provides a completely linked marker, it is possible to identify even very slight differences due to the R alleles, as distinguished from the effects of modifying factors.

The series is non-linear, in that various cases occur in which one allele produces distinctly more effect than another upon some tissues and distinctly less upon others. Such cases might be expected to occur if the alleles differ only in the extent of their effect upon some single reaction, for it might be expected that pigmentation would increase with "strength of action" up to a given point and then decline, and that this optimum point might differ in the various tissues concerned. The effects observed do not fit this hypothesis in any reasonably simple form. They suggest rather that the effect of R alleles upon plant color is a complex of two or more types of action, independent in the sense in which the aleurone color effect and the plant color effect are independent.

For a major portion of the plant color effect, however, the reaction of different tissues is quite closely correlated. The R^r alleles may be arranged in a single sequence to represent their effect upon occurrence and intensity of pigmentation in mesocotyl, coleoptile, seedling leaf tip and margin, seedling leaf sheath, mature plant basal sheaths, tassel glume, and anther. For example, the occurrence of seedling leaf tip color marks a level beyond which full anther color is developed and below which anther color is distinctly weak. Full coleoptile and mesocotyl color are reached below this level, though the color of these organs is deeper and more rapidly developed in the types with tip color. Distinct seedling sheath color does not occur until a higher level is reached, and is accompanied by deepened coloration of the tassel glumes and anthers. In their effect upon this character complex the R alleles studied may be regarded as differing merely in level of action, and the varying thresholds of response in the tissues studied provide a sensitive means of detecting differences in the level of action of the alleles compared.

L. J. Stadler and Seymour Fogel

2. New Alleles of A. As previously noted (News Letter, 1941: 44) the gene A^b mutates spontaneously at a fairly high rate to a type resembling a^P. The mutants, identified by the pale aleurone effect, produce plants which like a^P produce both anthocyanin and anthoxanthin pigment. Nine of the mutants were checked for the dominant brown pericarp effect present in A^b and a^P, and all showed this effect also.

In plant color with B and Pl, the mutants were in general more deeply colored and more reddish than the standard a^P. They varied rather widely in degree of redness, ranging from a deep brown to a maroon shade approaching purple at maturity. The original mutants, and various others which have occurred in later experiments with A^b,

form an apparently continuous series between the two extremes. No mutant of \underline{A}^b to a colorless aleurone type or to a type producing only anthoxanthin pigment in the plant has been found.

Four representative mutants were selected for further study, to determine whether the differences in expression were due to differences in the mutant alleles. The factor et, an X-ray induced chromosome 3 mutant, located 11 units distal to A, was combined with one of the mutants and also with standard \underline{a}^P , and the phenotypic effects were compared in backcross progenies in which the various alleles could be compared in plant color (with B and Pl) in sib plants. The results show that the four mutants represent distinguishable alleles of A, each producing a mixture of anthocyanin and anthoxanthin pigments but differing in the relative quantity of anthocyanin produced. These are designated mahogany (\underline{A}^{b-m}), cedar (\underline{A}^{b-c}), chestnut (\underline{A}^{b-ch}) and walnut (\underline{A}^{b-w}).

The aleurone color of the mutant \underline{A}^b 's described, as identified in et-marked segregations, is paler than that of \underline{A}^b or A, but not so pale as \underline{a}^P . Seed separation may be made effectively in segregations against either A or \underline{a}^P . There is also a recognizable difference in aleurone color between some of the mutant types, which sometimes is distinct enough for individual classification.

There are some interesting differences in the action of these pale aleurone mutants of \underline{A}^b and the two pale aleurone mutants at hand which arose from other members of the A series. \underline{A}^{lt} (News Letter, 1941: 46) is an ultra-violet mutant of A, which has a pale aleurone and reddish purple plant color, yielding anthocyanin and anthoxanthin pigment. \underline{A}^w is a mutant of a, which occurred as a sector with pale purple anthers in a plant of a Dt B Pl Rf. It also produces pale aleurone and a reddish plant color, yielding anthocyanin and anthoxanthin. Qualitative tests show a distinct difference in the anthocyanin produced by \underline{A}^{lt} and \underline{A}^w , on the one hand, and by \underline{A}^{b-m} , \underline{A}^{b-c} , \underline{A}^{b-ch} , \underline{A}^{b-w} , and \underline{a}^P on the other.

The pale \underline{A}^b mutants, like \underline{a}^P , show little or no difference in the aleurone color of homozygous seeds vs. seeds heterozygous for a. Both \underline{A}^{lt} and \underline{A}^w , in selfed ears of plants heterozygous for a, show clearly cumulative effects, the heterozygous seeds being distinctly pale and the homozygous seeds often being indistinguishable from full A.

In compounds among the pale \underline{A}^b mutants and between these mutants and \underline{a}^P , the plant color effect of the redder member is distinctly dominant, and in those cases in which aleurone color is distinguishable the darker type is dominant. \underline{A}^{lt} produces a redder plant color than the \underline{A}^b mutants or \underline{a}^P , but the hybrid $\underline{A}^{lt}/\underline{a}^P$ is intermediate, with a pronounced increase in anthoxanthin content. $\underline{A}^{lt} \times \underline{a}^P/\underline{a}$ yields progeny of two very distinct types, the $\underline{A}^{lt}/\underline{a}^P$ plants showing a distinct dominant effect of \underline{a}^P on anthoxanthin production as compared with the $\underline{A}^{lt}/\underline{a}$ sibs. This dominant effect of \underline{a}^P is not evident in crosses with A or \underline{A}^b , so far as the appearance of the plants is concerned. It is evident, however, in crosses with \underline{A}^{br} , a Dt-mutant obtained by Rhoades, (News Letter, 1941: 6)

which resembles A in plant and aleurone color but does not give red pericarp. In crosses of A^{br} x a^p/a there is a distinct diminution of red and increase of brown in the plant color of A^{br}/a^p vs. A^{br}/a sibs. A similar effect is shown by cedar, chestnut and walnut, the only A^b mutants tried in this combination. It is wholly absent in A^{br} x A^{lt}/a, the A^{br}/A^{lt} plants being indistinguishable from the A^{br}/a sibs.

3. The Action of R and B. No anthocyanin pigment is produced in maize except in the presence of suitable alleles of A₁, A₂, and either R or B. For certain tissues B will serve as well or better than R; for others R is essential regardless of the presence of B. In those tissues which may be colored by the action of either R or B, the essential step in anthocyanin synthesis which is accomplished by R must be accomplished also by B, or it must be made unnecessary by some alternative step accomplished by B.

The effects of varying R action are shown by the phenotypes of the various R alleles, and a similar comparison may be made for B by comparing it with the weakened B alleles described by Emerson in 1921. Several additional B alleles intermediate in action between B and b have been picked up in exotic strains and in dent corn varieties. Their study is not quite as convenient as that of the R alleles, but is facilitated by the use of Anderson's chromosome 2 inversion to intensify the linkage with seedling markers. The B alleles, like the R alleles, differ in the occurrence and the intensity of the pigmentation of various organs, and in their major plant color effect they may be arranged in a single sequence of increasing strength on the assumption of different thresholds of response in different tissues. The order of response of the different tissues is however quite different from that found for the R alleles. The standard B used produces rather strong pigmentation of the seedling leaf sheath, coleoptile and mesocotyl, and deep pigmentation of the mature sheath, blade, culm, tassel, and cob. With successively weaker B alleles, blade color is restricted to the midrib and soon disappears, sheath color becomes weakened first in the lowermost sheaths and last in the middle sheaths. Glume color diminishes first at the tip region of the glume, and with successive steps is limited more and more closely to the base of the glume. In the weakest allele distinguishable from b, plant color is limited to a narrow transverse line at the base of the glume and to scattered streaks of color on the culms and sheaths of the middle internodes of the plant. The pigmentation of mesocotyl, coleoptile, and seedling sheath disappears early in this sequence, and most of the alleles give wholly colorless seedlings.

The response of R and B genotypes to sugar feeding of excised tissues (News Letter 1942: 31; Amer. Jour. Bot., 29: 17s) is sharply different. Sib plants of r^{ch} b and B r^g (with A₁, A₂, P₁) are about equally colored in coleoptile and seedling leaf sheath. In later growth the latter becomes much more deeply colored in leaf sheath and blade. Excised leaf sections of the r^{ch} plants, in seedling or later stages, produce anthocyanin abundantly with externally supplied glucose, the amount of anthocyanin varying with the glucose concentration. Seedling leaf sections of the B

plants produce no anthocyanin, regardless of the glucose concentration, and leaf sections taken at a stage when anthocyanin is being produced in the leaf show no effect of added sugar upon the rate of anthocyanin production. The presence of B in addition to r^{ch} does not increase the rate of anthocyanin production by the excised leaf sections, and the addition of B to weaker alleles of R, which produce anthocyanin at a lower rate than r^{ch} , does not increase their response to added glucose.

L. J. Stadler

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1. The number 4 trisome is now available in a stock segregating for su 1. Also, all of the other trisomes, with the exception of number 1, are available in vigorous stock cytologically determined to be free of B chromosomes. To make these trisomic stocks more suitable for use in the corn belt and elsewhere, they have been outcrossed to different commercial inbred lines, including the corn belt lines Hy and 187-2 and somewhat earlier maturing New York State lines of Luces Favorite and Cornell 11.

2. The embryo culture technic was utilized to obtain hybrids of tetraploid corn and tetraploid *Tripsacum*. Tetraploid corn was pollinated with a mixture of pollen from $4n$ corn and $4n$ *Tripsacum* by stripping down the husks and sprinkling the pollen over the silks exposed throughout their entire length. The husks were then drawn up about the ear shoot and held in place with rubber bands and a glassine bag to prevent excessive evaporation. Ears pollinated in this manner were harvested 18 to 21 days after pollination, the embryos of the partially developed kernels were excised and transferred to a sterile agar nutrient medium in 2 oz. bottles. After their root systems were well established, usually after 10 days to 2 weeks, the seedlings were transplanted to soil. The 56 chromosome hybrids are slow-growing and thus far show no evidence of hybrid vigor. At the present time (January), $4n$ corn plants of the same age and similarly derived from excised embryos originating from pollinations made last August have passed the silking and pollen-shedding stage, while the hybrids are still making exclusively vegetative growth and show no evidence of stem elongation, although they are sturdy, healthy plants. Since these *Tripsacum*-corn hybrids, unlike those previously obtained by Mangelsdorf and Reeves, have two sets of chromosomes from each parent, they should be highly fertile; but this remains to be seen.

3. Tetraploidy may be induced in the shoot apex of very young maize seedlings by introducing a dilute aqueous solution of colchicine through the cut end of the primary seminal root, or later in seedling development after the secondary seminal roots are established by introducing the colchicine solution through the base of the epicotyl following excision of the seed. Immersion alternately in .05% colchicine and water for 24-hour periods, usually for 4 days, effectively induced sizeable sectors of $4n$ tissue that persisted to maturity and affected both tassel and ear shoot. In some instances both ear shoot and tassel apparently were entirely tetraploid, and selfing such plants produced tetraploid seed. External applications of colchicine to ear-shoots and seedlings prove

unsatisfactory as a practical method of chromosome doubling.

This seedling treatment technic is being adapted to the production of diploids from haploids in an attempt to obtain homozygous diploids from heterozygous maize stocks, especially commercial hybrids, in one generation.

4. The origin of the perennial rhizome habit of *Euchlaena perennis* Hitch. has puzzled students of species relationship in the tribe Maydeae for many years. All other American representatives of the tribe are annuals, with the exception of *Tripsacum*, which is perennial but grows in dense clumps and has very short rhizomes unlike the elongate freely-spreading rhizomes of perennial teosinte. The annual teosinte of Central America and Florida that has been examined cytologically is diploid. The perennial teosinte, known only from one very restricted area in Mexico, is tetraploid and has multivalent synapsis of its chromosomes and other characteristics which indicate that it is either a true autotetraploid or an allotetraploid of two closely related species or ecotypes.

Diploid forms of perennial teosinte and tetraploid forms of annual teosinte are unknown in nature. However, a somatic mutation from the annual to the perennial habit occurred in a plant of Durango teosinte grown in the greenhouse in 1931. The annual portion of this plant (1359-10) was diploid and its selfed progeny were diploid annuals with the exception of one plant (1625-B-1), which was tetraploid and perennial. The perennial rhizome sector of plant 1359-10 was propagated vegetatively, and several root-tips collected from it soon after it was discovered were examined cytologically and found to be entirely tetraploid. However, of 15 seedlings produced during the following flowering period from selfed seed of the perennial mutant one was triploid and 14 were tetraploid, and the mutant pollinated during this same period by tetraploid corn produced 11 tetraploids and one triploid, suggesting that diploid tissue persisted in the mutant sector up to the time the first crop of seed was produced sufficient to form at least 2 female gametes with a monoploid set of chromosomes.

The spontaneous occurrence of this somatic mutation from the annual diploid to the perennial tetraploid condition was interpreted as strong evidence in support of the assumption that *E. perennis* was simply a tetraploid mutant of *E. mexicana*.

To test this assumption further, tetraploidy was induced experimentally in stocks of Durango, Chalco and Florida teosinte with the heat-treatment technic. These artificial tetraploids had the annual growth habit of the parent diploids and exhibited no perennial characteristics whatever.

Another test of the relation between tetraploidy and the perennial habit involved the identification of parthenogenetic diploids in the progeny of *E. perennis* to determine whether they would be annual or perennial. In diploid maize parthenogenetic haploids occur with an average frequency of about 1:2000, and in tetraploid maize parthenogenetic diploids occur with an average frequency of about 1:1000. Data from greenhouse material of perennial teosinte (teosinte is a short-day plant which normally flowers during November in this latitude) accumulated during the past 10 years

indicate that haploid parthenogenesis is extremely rare in this species. In this experiment, the results of which are summarized in the accompanying table, various stocks of perennial teosinte were used, including a culture from rhizomes collected at the type locality in Mexico (El6-515), a seedling from seed harvested from the type material in Mexico (El3-533), selfed progeny of El6-515 (2660), selfed progeny of El3-533 (2661), the spontaneous tetraploid mutant (1359-10) and the tetraploid seedling (1625 B-1) from the annual portion of this plant.

Seedling progenies obtained from various perennial
teosinte X diploid corn crosses, 1932-1941

Perennial teosinte stocks								
El3-533		El6-515	1359-10	1625 B-1	2660 16-515 selfed	2661 13-533 selfed	3449 2661 selfed	Misc.
1932	15	80	42					
1933	1028	1417						
1934	565	126	485	317	1132	1141		428
1935	570	860	875	784	1040	415		
1936	149	1263	166	22	117	1156		
1937	16	1410	142	34	143	1081		137
1938	91	1345	310	47	265	1524		
1939		1125	263	44		1695	197	
1940	134	405	11	68		2490	20	
1941	177	1148	320	43	754		89	140
Totals 2745		9179	2614	1359	3451	9502	306	705
Grand Total		29,869						

and one parthenogenetic paternal haploid were identified among the 29,861 seedlings from the perennial teosinte X diploid corn crosses grown during the period from 1932 to 1941 inclusive. The maternal diploid appeared in the 1936 progeny of culture 2661, which in that year contained 1156 seedlings. This exceptional diploid had the annual growth habit. It tillered profusely, but produced no rhizomes and after forming a few aborted tassels the plant died at about the same time annual teosinte plants of the same age mature and then die. The parthenogenetic haploid of paternal origin had narrow leaves and otherwise resembled teosinte in the early seedling state, except that it was a diminutive seedling and had the purple color of the pollen parent; later in ontogeny it became typically maize-like and was indistinguishable from ordinary maternal haploids of the same stock.

In addition to these two exceptional seedlings there occurred each year a small number of maternal tetraploid seedlings. These were at first assumed to be contaminations, but the prevalence among them of recessive chlorophyll mutants suggested that at least some of them may have originated from unfertilized, normally-reduced diploid eggs followed by chromosome doubling in early embryogeny. If this is happening, it would help to explain the low frequency of maternal diploids obtained from this perennial teosinte X corn cross.

The perennial rhizome habit of *E. perennis* does not behave as a simple Mendelian recessive. The F_1 *perennis* X $4n$ corn is intermediate in that it can be maintained by careful subdivision and occasionally produces short rhizomes. The character does not segregate sharply in F_2 and back-cross progenies but behaves like typical quantitative characters that are dependent on the interaction of multiple factors. In these segregating progenies most of the plants tillered much more profusely than did the $4n$ corn parent, but very few developed any appreciable rhizome system during the summer season. A much longer growing season than we have at Ithaca is needed to make really satisfactory classification for rhizome habit in material of this kind. However, it is apparent from the general character of the segregating populations and the intermediate nature of the F_1 plants with respect to rhizome habits that a dosage effect is involved, and it is therefore conceivable that cumulative gene action accompanying chromosome doubling might transform an annual into a perennial in the presence of a suitable genotype.

Some such interpretation of the origin of the perennial rhizome habit of *E. perennis* is supported by the occurrence of the parthenogenetic maternal diploid lacking the perennial rhizome habit in the progeny of *E. perennis*, and by the occurrence of the spontaneous perennial, tetraploid chimera in an annual plant of *E. mexicana*. The persistence of the annual habit in the experimental autotetraploids of *E. mexicana* may mean that the stocks from which they were produced lacked the essential genes requisite to the production of the perennial habit in the tetraploid state. It is generally believed that most annual forms of teosinte possess admixtures of maize genes. This would provide ample opportunity for displacement of genes of annual teosinte having perennial prepotencies by maize genes with strong annual prepotencies and would account for the appearance of the perennial habit in some annual teosinte tetraploids and not in others.

L. F. Randolph

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El Valle, D.F., Venezuela

1. Corn Breeding in the Tropics. Perhaps a few observations on corn breeding in Venezuela, latitude N 12, would be of interest to geneticists in other parts of the world.

A preliminary survey of the existing corn varieties in Venezuela made in September, 1939, revealed that all of them were of inferior productive capacity with a tendency to grow extremely tall and set the ear high on the stalk. Most varieties had white seeds, primarily because the people depend to a large extent on "arepa", ground corn in the form of a small, thick pancake, for food. Yellow "arepas" are preferred in some regions of the country, but white "arepas" are more commonly used. For years, negative selection has been going on in corn because the people eat the best seeds and plant the leftovers.

Some of the best varieties and hybrids from the United States and from many tropical and subtropical countries, including Cuba, Puerto Rico, Santo Domingo, and Colombia, were collected and planted together with the Venezuelan varieties in three different experiment stations. The types from the United States were vigorous in the seedling stage but they came into flower too early, as was expected, due to the difference in length of day. They became weak and were attacked by many diseases and insects. A Puerto Rican variety, Mayorbella, obtained from Dr. Arturo Roque, was vigorous in the seedling stage, then became weak, and later vigorous again and produced relatively large ears. The Venezuelan varieties gave their usual rank plant growth but did not set desirable ears. A yellow seeded type from Cuba with sturdy stalk of medium height set two ears at the proper distance from the ground. This type outyielded the others by at least 100 per cent. In further tests it has made the unusual performance of giving relatively high yields all over Venezuela from altitudes of 40 feet to 4,000 feet. In three years in which six generations of mass selection have been made, it has become the most popular variety in the country in spite of its color.

Its origin is interesting. A representative from this government collected two varieties from Cuba in 1938, but the seeds of the two were mixed in handling. About two years later several hundred sound seeds were salvaged from a bag of weevil-eaten material, and from these seeds the present selection has been developed. This selected type is being distributed in this country and in other neighboring countries under the name of VENEZUELA-1.

The main project is the development of hybrid corn adapted to the climatic conditions of Venezuela. Six generations of inbreeding of the heterogeneous material has resulted in approximately 300 selected lines, some of which have a desirable appearance and have done well in topcrosses and single crosses. The first double crosses are now being tested.

It is interesting to note that most of the varieties collected from Venezuela and other countries of this latitude degenerate rapidly with intensive inbreeding. Outcrossing followed by sib crossing has been

accepted as the best practice for utilizing these varieties.

The Cuban type is a striking exception to this rule. Selfing has resulted in a multitude of types, but most of them are relatively vigorous and some are exceptionally impressive.

Inbreeding has resulted in the usual number of hidden recessives and the isolation of new mutations. Male sterile, barren stalk, brown midrib, virescents, white seedlings, zebra, tassel seed, cuzcoid, and many others have been observed.

A small but important change in breeding technique has been necessary due to the larvae of an octitud fly, Euxesto stigmatia Loew. It is not advisable to cut back the husks of the ear shoot to obtain a uniform brush of silks because the insects enter and destroy the ear. It is better to wait as long as possible for the silks to come out naturally before pollinating.

There can be no doubt that in the near future hybrid corn will be available for distribution in a country which has no seed companies and little knowledge of seed improvement. In the meantime, however, the type VENEZUELA-1, improved by mass selection, has been widely distributed.

2. Sweet Corn in Venezuela. The mutation to sugary corn which occurred in a variety of dent corn adapted to the climatic conditions of Venezuela (Maize Genetics Cooperation News Letter, April-1, 1941) has been the basis of the development of sweet corn in this country. This corn has been named VENEZUELA-2 and is now widely distributed throughout the entire country and in other South American countries that have requested it. Some of the details of its development may be of interest.

Until 1942, the majority of the people in Venezuela had never tasted true sweet corn and most of them had never heard of it. Some who had travelled in the United States, imported seeds of a few varieties and planted them in Venezuela, but the plants were always weak, badly diseased, attacked by insects and consequently unable to produce ears.

Corn known as "jojotos" has always been consumed in Venezuela and is sold in the markets of the cities. This is the native type, a mixture between dent and flint, that is harvested not in the milk stage but in the soft dough stage. It is eaten directly from the cob or cut off and used to make certain Venezuelan dishes such as "cachapas", a pancake-like preparation. The true sweet corn now available in Venezuela has such a contrasting flavor to the dent-flint mixture that it is widely accepted by the people of all classes.

In 1939 when a modern program of corn improvement was initiated in Venezuela, approximately 3,000 self pollinations were made in the best local and imported varieties to develop inbred lines. Some of the first generation ears were planted in progeny rows in 1940 and about 3,000 of the best plants were selfed. None of these second generation ears segregated for sweet corn. But one of the second generation plants gave, on selfing, an ear with 216 starchy kernels and 73 sugary kernels. Five plants in the same progeny gave ears with only starchy kernels.

Since there had been no sweet corn planted anywhere near these fields and no sugary kernels had appeared in the first two generations of inbreeding, it is extremely likely that this was a mutation to sweet corn.

Fortunately, it occurred in one of the most vigorous lines which had such desirable characters as deep green color, relatively early maturity, two ears per stalk and, most important of all excellent husk covering of the ears.

Some of the sugary seeds and the starchy seeds from this ear were planted and self-pollinated. As was expected the sugary kernels gave ears of 100% sugary type, whereas some of the starchy kernels bred true for starchy and others segregated sugary. Seeds from the sugary ears were planted. When these plants had tassels and pollen, a field of the original variety of starchy corn was nearing the completion of its flowering period. Ten plants in this field were pollinated with pollen from the sweet corn inbred. The seeds from these ten ears were mixed and planted in a small field at the Instituto Experimental de Agricultura y Zootecnia in January, 1942. Vigorous plants were obtained. There was no attempt to control the pollination. All of the ears segregated approximately 25 per cent sugary kernels.

The sugary kernels from these ears were planted in one field and the starchy kernels in another. There was no attempt to control the pollination in either field.

The ears harvested from the first field were of the sugary type, but there was considerable variation in the kernels. Some of them were entirely translucent while others showed various degrees of starchiness.

In the second field where theoretically one-third of the seeds planted were homozygous starchy (Su Su) and two-thirds heterozygous for sugary (Su su), the expected ratio of starchy to segregating ears was 1:2. Actually, there were 9,347 ears with all the kernels starchy and 22,147 ears segregating for sugary.

Theoretically, the segregating ears should have had a ratio of 5 Su to 1 su kernels. One hundred of these ears taken at random gave ratios from 20 Su : 1 su to 3 Su : 1 su, but the total count was 39,742 Su kernels and 9,099 su kernels, or a ratio of 4,36 : 1. This discrepancy from 5 : 1 ratio is probably due to a position effect of the plants in the field.

On October 7, 1942 a demonstration of the history of sweet corn in Venezuela was made to an audience in the auditorium of the Sociedad Venezolana de Ciencias Naturales. At the close of the demonstration, packages of the new sweet corn were distributed to all present. Considerable seed has been distributed since then.

From a scientific point of view this sweet corn will not be of maximum yield because it is the third generation of a cross between an inbred line and a variety. In spite of this, however, it is being distributed because it has yielded sufficiently well to give the public a taste of sweet corn.

Since the first ear of this corn was discovered it has been crossed with a number of selected varieties of ordinary corn which do well under the climatic conditions of Venezuela. The plants from these numerous crosses have been self-pollinated, and inbred lines are being developed in a number of types. When there is an abundance of inbred lines involving the sugary gene, they will be crossed to give hybrid sweet corn for Venezuela. In the meantime the other topcross type will be propagated.

D. G. Langham

Harvard University, Cambridge, Mass.

Studies of chromosome knob numbers of the maize varieties of Latin-America have been continued with the following results:

Country	No. Varieties	Range in Knob No.	Ave. Knob No.
Brazil	8	5-9	6.6
Colombia	2	12-13	12.2
Costa Rica	4	10-12	11.0
Cuba	6	11-12	11.2
Mexico	33	4-13	10.0
Nicaragua	15	9-14	12.8
Panama	4	12-14	12.6
Paraguay	5	2-6	4.8
Peru	15	1-2	1.3

Although the sampling of individual countries is still far from adequate, the data tend to support the previous conclusion, that low-knob varieties are confined in Central America to Western Guatemala and to the immediately adjoining regions in Mexico. In all other parts of Central America and Mexico and in Cuba as well, only high-knob varieties have been encountered. Western Guatemala and the adjoining state of Chiapas in Mexico continues to appear to be the center of maize diversity in Central America.

It appears also that Paraguay must now be added to Peru and Bolivia as a region of low-knob varieties in South America. Although only five varieties from Paraguay have been examined cytologically, the majority of varieties collected are of the same general type as these and will probably prove to have but few knobs.

Dr. Hugh C. Cutler has now spent more than a year in Brazil, Paraguay and Bolivia collecting native corn varieties and searching for wild maize. His first goal is being successfully achieved; the second is still elusive. Several reports of maize growing in the wild have been investigated with wholly negative results. The "wild" maize in each case was either cultivated maize obviously escaped from cultivation or not maize at all. The cultivated corn collected from Paraguay and

Southwestern Brazil is of considerable interest. The cobs are quite flexible; the pedicels on both staminate and pistillate spikelets longer than normal.

A variety of maize obtained from Amantina Island in Lake Titicaca in Peru at an altitude of about 12,500 feet, probably the highest altitude at which corn is grown in any part of the world has proved to be early and cold-resistant. These characters may make it valuable for plant breeding in spite of the fact that it is very susceptible to smut.

P. C. Mangelsdorf and James W. Cameron

There is presented here a partial list of publications on maize.

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III. Inventory of Seed Stocks Propagated in 1942

In 1942 I planted and hand-pollinated only such stocks as were sent me last spring or as Dr. Welch told me should be replenished. A total of 140 ears were obtained.

- Co 42-1 $++$ p as $\frac{GS}{+}$ +/sr $\frac{+}{ts2}$ p + + $\frac{bm2}{+}$. 9 ears.
- " 42-2 + p as $\frac{GS}{+}$ /sr PWR + +. 7 ears.
- " 42-3 as/42-1. 5 ears.
- " 42-5 zb6 (from Burnham). 3 ears.
- " 42-6 br, smut resistant stock (from Burnham). 3 ears.
- " 42-7 A C R Pr cr, brown pericarp (from Burnham). 5 ears.
- " 42-8 A C R pr cr (from Burnham). 3 ears.
- " 42-9 a C R pr cr (from Burnham). 1 ear.
- " 42-10 } F₂ of a C R $\frac{na}{+} \frac{ts4}{+}$ (from Burnham). 14 ears.
- " 42-11 }
- " 42-12 $++$ / $\frac{bt2}{+} \frac{bt4}{+}$ (from Burnham). 10 ears.
- " 42-13 } T3-9a C sh + + / pr Sh wx (from Burnham). 19 ears.
- " 42-14 }
- " 42-15 Homozygous T3-5d (from Shuman). 7 ears.
- " 42-16 T3-5d/+ (from Shuman). 4 ears.
- " 42-17 P gs bm2. 3 ears.
- " 42-18 P br f bm2. 2 ears.
- " 42-19 Tu/+. 3 ears.
- " 42-20 su $\frac{Tu}{+}$. 1 ear.
- " 42-21 $\frac{Tu}{+}$ gl3, segregating ws2. 7 ears.
- " 42-22 } su $\frac{Tu}{+}$ gl3. 5 ears.
- " 42-23 }
- " 42-27 } su la. 3 ears.
- " 42-28 }
- " 42-31 y4 It a c r pr i. 3 ears.
- " 42-32 } y4 It/Y4 it. 14 ears.
- " 42-33 }
- " 42-34 }
- " 42-41 I wx yg_b . 9 ears.

Supplement to News Letter 17

Two reports received too late for inclusion with the others are:

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University of Minnesota
University Farm, St. Paul, Minnesota

1. There is an indication of linkage between interchange 1-9c (breaks near P_1 and wx-13-T), and the dominant white cap (W^C), a small backcross population having:

W^C = 12 normals + 29 semisteriles; yellow cap = 27 normals + 13 semisteriles; or about 35% c.o. \pm 5% S.E.

2. Dr. Sprague furnished us with a complete set of his glossy testers. As reported last year, the Coop gl 10 is the same as Hayes' gl 4 (shows 8% c.o. with wx). Tests show it is genetically different from Sprague's glossy 1, 2, 3, 4, 5, 6, 8, 9, 10 (probably different from 7), leaving gl 11 and 12 to be tested.

Also:	Coop gl 3	- same as Sprague gl 3
	" gl 5	- " " " gl 5
	" gl 8	- different from Sprague gl 8

3. Crosses between interchanges involving the same two chromosomes were studied for pollen and ear sterility and as a possible source of viable deficiencies. If two are crossed which involve exactly the same loci in the two chromosomes, the F_1 should show no sterility.

Where the breaks are not at the same loci, the result depends on the positions of the breaks relative to the spindle fiber. In certain cases gametic combinations should be possible which carry a deficiency for the piece between the breaks.

In a series of such crosses, one showed about 20% sterility and another 25% where the parents crossed with normals showed semisterility. Variation in size of the filled pollen grains was observed. Crosses with genes which have a chance of being near these loci have been made for deficiency tests; also crosses with sifted pollen.

4. Stocks of zebra-1, zebra-2, and zebra-3 have been revived from some old crosses made at Ithaca in 1929 or 1930. (These will be turned over to the Coop)

C. R. Burnham

"Luiz de Queiroz" - University of São Paulo
Piracicaba, São Paulo, Brazil

Since North American colleagues probably are not familiar with the working possibilities in the relatively new Department of Genetics and Cytology at Piracicaba, a few words will be said about it. Our College is situated in relatively flat country at 500 m. altitude and with a subtropical climate. There is a difference between summer and winter, more due to the difference of rain than of temperature. The total rainfall is of about 1 m. per year, but from June to September there is hardly any rain; but morning fogs from the river and heavy dew give still much moisture. Tropical crops grow well in the hot and rainy season (December to March) while cabbages, carrots, sweet peas, snapdragons, etc. grow in the winter and dry season (April to

September). The main crops of the region are sugar cane and oranges.

With irrigation corn may be grown practically the whole year around but we prefer, in order to get good ears, consecutive sowings from October to early February. There are only a few fungus diseases, and none of them serious. Insect attacks are generally only of small scale, though the sugar cane borer has recently become rather dangerous. The only really serious problem is the large scale attack by the grain weevils and moth, especially now with the difficulties of obtaining naphthaline.

1. Breeding Experiments

Ordinary Brazilian corn is composed of extremely heterogeneous and hardly improved varieties. Many of them seem to be equal or even inferior to the corn still grown by "wild" Indians. Modern breeding work has been started at Campinas and at Piracicaba.

A - Sweet Corn (Pedigree breeding): Sweet corn is practically not grown in Brazil and the imported strains which we have been able to observe hardly survive for more than a few generations. Since I had been engaged, while in England, in breeding for earliness, the scope of the experiment had to be revised completely. Extracts from the cross: (Tirol (white flint) x Golden Bantam) x Banting (Canadian, white early) were crossed with "Santa Rosa" (white dent) and with "Cateto" (orange flint) and we have now obtained several good lines of yellow-orange and of white sweet corn, well adapted to field conditions and resisting the heavy rains and winds; with mean plant height (without tassel): 2 m., mean height of ear: 1.2 m., time from sowing to silking: 65 days, one or two ears per stalk, absence of tillers, mean ear weight (dry): 100 g.

B - Early Corn (Pedigree breeding): Brazilian corn is very slow in growing, producing generally very tall plants with the ears at about $\frac{3}{5}$ to $\frac{2}{3}$ the height of the plant. Crosses were made between extracts of "Tirol x Early Canadian" (white flint, 40 days from sowing to silking) with Santa Rosa (white dent, 70-80 days to silking) and Cateto (orange flint, 60-70 days to silking.) It was not possible to combine tallness and earliness and it was difficult to suppress completely tillering in the early lines. Reasonably well adapted lines were obtained with the following characteristics; 45-50 days to silking, plant without tassel, 1.3 m., ear height 50 cm., mean ear weight 70 g per ear. Since the plants are completely different from the local varieties, it seems doubtful if these lines will be acceptable to the farmer, especially since earliness is not a necessity in the State of São Paulo.

The experiment was used to study the segregation of quantitative characters and to try out methods of statistical analysis. Some results may be summerized:

The standard error of distribution can be used as a measure of variability only if the means are of more or less the same magnitude. In order to compare P, F_1 , F_2 , etc.; a weighted measure has to be used. As can be shown theoretically, and has been proven experimentally, the coefficient of variation (standard error of distribution/mean x 100) should not be used,

but instead, a term called the "variance index": (standard error of distribution/square root of mean). Using this term, it can be shown for this index that, as expected:

$$(P) = (F_1) \quad (F_2) \quad (F_3) \dots\dots\dots$$

The segregation for earliness can be shown only by comparing F_3 families. The inevitable phenotypic variation with an error of more in F_2 .

In studying the relative position (height) of the ear, the ordinary coefficient of linear correlation r is of no use. The correlation for plant and ear height was found in all lines, hybrids or segregates, to be nearly constant and equal to 0.6 (positive and significant). However the index: "ear height"/plant height" should be used and it varies significantly with the following values: imported early lines 0.20, Brazilian commercial lines 0.60, some native corn up to 0.7 or 0.8 improved corn 0.5.

F. G. Brieger

C - Inbreeding and Outbreeding: Inbreeding was started in 1936 with "Santa Rosa", a commercial variety of white endosperm, essentially to obtain material for the demonstration of the value of the method. Single and double crosses are being carried on and a new population composed of several single crosses is also being tried. Recently work on orange flint and on orange dent corn was started also.

E. A. Graner

D - Population Breeding: Since it was thought that the method of pure-line breeding and subsequent crossing is a method too lengthy and costly for the actual status of maize growing here, an intermediate method is being tried out. Brazilian commercial corn is extremely heterogeneous, contains many defective plants and shows many undesirable traits. A vigorous selection was carried out, combined with selfing during a few (2-3) generations, and finally followed by sib and strain crossing. The results thus far obtained in small plots seem satisfactory and better than those obtained by mass selection without controlled pollination, though inferior, especially in homogeneity, to authentic hybrid corn.

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E - Late Sugary Strains: Some good sugary strains, very late for Connecticut, were given to us by Dr. W. R. Singleton and are now growing in our department. They include a strain segregating for a very late type that does not flower there but is expected to flower here. The plants in the field are now 40 days old.

E. A. Graner

2. Experiments about the Origin of Corn

A - Native Indian Corn: We were able to obtain through the help of Brazilian colleagues, of Dr. Cardenas of Cochabamba and of Dr. Cutler, authentic "wild Indian" corn. The Bolivia corn from Cochabamba grew very well at the low altitude of Piracicaba, flowered generally well, but

produced very poor ears. Material from the lowlands of Mato Grosse (Brazil), from Paraguay and the Bolivian Chaco is much more satisfactory. But in nearly all cases it was rather difficult to maintain the strains, since they degenerate very rapidly with more or less close inbreeding. The following material has been studied genetically.

"Acre" from the territory of Acre (Brazil). The plants are very tall without tillers, ears long and slender with 8 rows, grains large, round and soft, exhibiting the following colors: dominant purple (ACR Pr), red (pr pr) or recessive colorless (probably rr), brown aleurone (lost), yellow or white endosperm.

"Chavantes" (from the State of Mato Grosso, Brazil). Very tall plants, segregating semi-dwarf, ears big and heavy, 12 or more rows, grains large, soft, white or sometimes tinged, purple (Pr), red (pr pr) or light pink (pericarp?). The constitution of these grains is probably AA CiCi RR as shown by the following test cross with C sh: (F₂):

	: C ⁱ - Sh	: C ⁱ - sh sh	: CC Sh -	: CC sh sh	: Total
obs.	: 861	: 34	: 61	: 187	: 1.143

The dominant inhibitor Cⁱ is not completely dominant and varying percentages of the kernels with the constitution Cⁱ-Sh- are not white, but very pale purple and red. It seems as a whole that the Indians selected modifiers which reduce all possible color in the kernels as much as possible.

White endosperm is only incompletely recessive to yellow and there is present some kind of pericarp color which however becomes clearly visible only after outcrossing.

"Diamantino" (from Mato Grosso, Brazil). We received three lots of seeds. In all of them the ears originally were heavy and many rowed. The color of grains varied.

Diamantino I, had deep red pericarp (P) segregating normally after crossing.

Diamantino II, had dirty brownish-orange kernels, due to orange, white or colorless pericarp on yellow-orange endosperm and sometimes yellow-brown aleurone. The segregation for pericarp color was interesting in so far as its existence could be verified only in some years, and in one year only classification between orange and colorless pericarp was very easy. In this year orange pericarp was in some instances so intense as to give a bright red color.

Diamantino III, contained colored and colorless aleurone over orange endosperm, sometimes covered by orange pericarp (white cob). Absence of aleurone color may be due either to a dominant or recessive inhibitor. The former is certainly an allele to the C factor as shown by the linkage test with CC sh sh. But there are a large number of modifiers acting and disturbing the ratios. The ears collected after selfing fell into two groups. In the first there was an excess of colorless-shrunken grains combined with a deficiency of the colored-shrunken grains. In the other group of ears, besides this deviation,

there appeared a deficiency in the number of the normal grains and a corresponding excess is the colored-shrunken grains.

	C ⁱ - Sh :	C ⁱ sh sh :	CC-sh :	CC sh sh :	Total :	250
	:	:	:	:	:	:
1st group	1.270 :	146 :	52 :	232 :	1.700 :	425
1st group	771 :	99 :	201 :	212 :	1.283 :	328
	:	:	:	:	:	:

Plant color in most strains of all three forms of native corn, Acre, Chavantes and Diamantino, is either dilute purple or dilute sun red. But the culm is very frequently heavily colored, and this color seems, at least partially, independent from A-B-Pl mechanisms.

In the shucks various colors were observed which may be either "sun red", deep purple, dilute purple, red and reddish-brown.

Finally, the glumes and the whole base of the grains may be deep or light purple or red, independent from cob color. Apparently somehow this color depends upon the same factors as the color of the shucks.

So far the existence of these different colors in vegetative organs has been registered; but it has not yet been possible, owing to lack of time, to start on a detailed genetic analysis.

If we take all characters into consideration, it seems that the indigenous strains from Mato Grosso together with the material collected by Cutler in Paraguay and the Bolivian lowlands form a natural group. Similar traits may be found also in local forms, cultivated in São Paulo. In all of them there appears, with more or less frequency, all or some of the following characters.

Slender and long ears with flexible rachis. Grains half covered by their glumes. Kernels more or less round or pointed, containing soft starch. Anthocyanin generally absent in the aleurone owing to the presence of inhibitors at the C-locus. On the other side there is a tendency for the appearance of brownish-orange colors, in the aleurone, endosperm, and pericarp.

Three characters seem to me especially important: the brownish-orange color of the kernels which may be considered as an approximation to a natural "wild" color, the slender and flexible rachis and the development of large glumes which may be taken as a change in the direction of pod corn. Their widespread occurrence can hardly be considered as a coincidence, in view of the old hypothesis, recently taken up again by Mangelsdorf and Reeves, that pod corn is the most primitive of all the different types of maize and that the lowlands on both sides of the Rio Paraguay, i.e., the triangle formed by lower Bolivia, western Mato Grosso and Paraguay, may be the geographic centre of the origin of maize. On the contrary, I think our observations, very briefly reported above, support strongly this hypothesis.

F. G. Brieger

B - Pod corn: Has been obtained from two sources. "São Paulo Pod" and "Bolivia Pod". The latter was sent to us by Dr. Cardenas and later by Dr. Cutler. The other type came from one ear left casually in our department

by a student and about which we know only that it came from São Carlos, that is from an inhabited and cultivated region only about 300 Km. from São Paulo and where we cannot expect to find "native Indian" corn. In all its characters, except of course being pod corn, it corresponds to the Brazilian corn of the region.

The studies of Bolivian pod corn are still in the beginning and we have met again the difficulties mentioned above, that corn from the Bolivian highlands grows well, but hardly produces ears in our altitude. Thus we can say only so far that it contains a dominant Tu gene.

São Paulo pod corn is also due to a dominant gene which is normally transmitted through the female while there is a strong selection against Tu-pollen tubes. At the most, half of them may eventually function, but generally less.

The original ear was large and well filled with a slender but very hard rachis. The seeds covered by large glumes, were small and more or less pointed and stood at the end of a long pedicel, of about the same length as the seed itself. The tassels of the first tunicate generation grown had drooping branches, with nearly normal or somewhat enlarged glumes and occasionally some silks.

Owing to the degeneration after inbreeding, the original line had to be outcrossed, and native Indian corn was used for this purpose.

The Tu ears in later generations varied very much, the extremes being silkless sterile ears, sterile ears with abnormally large glumes, ordinary fertile Tu ears and, finally, fertile ears with the kernels hardly covered by their glumes. The rachis remained always thin and rigid. In extremely large fertile ears the circumference necessary for the base of the kernels differed very much from the circumference of the rachis. In these cases the rachis split open lengthwise, the rows of grains remaining together in fours, with one group of two remaining when the total number was not a multiple of 4.

A successful selection was carried out to increase femaleness in the tassel. Finally a heavily bearded tassel was obtained with some 400 seeds and in its offspring the majority of all tunicate plants were again heavily bearded. In some cases it seems that each spikelet contained at least one female or perfect flower.

These hermaphroditic tassels were very large and drooping from the beginning. With the setting of seeds they became very heavy and tended to upset somewhat the balance of the plants. But one must not forget that a tassel with a total length of 40 cm. is small on a plant of over 3 m.! There seems to occur in these tunicate plants an increase in the number of nodes between tassel base and ear, but the internodes remain short and the corresponding leaves show transformations in the direction of shucks.

However the most interesting transformations are to be found in the structure of the spikelets. The ordinary spikelets of the tassel with two male flowers are substituted, in different tassels, by a large variety of other combinations: 1 male or sterile and 1 female or perfect flower,

2 female flowers, 1 female and one perfect flower. But the most outstanding cases occurred in the spikelet of one tassel where one male flower was followed by up to four female flowers. At the same time a tendency appeared for splitting the ends of the individual silks into two arms, often of unequal size. Thus the Tu gene causes the appearance of characters long lost in the group of the Maydeae and the related Andropogoneae: many flowered spikelets.

The observations, reported above were mainly made on plants heterozygous for Tu. Owing to the elimination of the Tu pollen tubes, the number of Tu-Tu homozygotes must naturally be small. The phenotype of the homozygotes registered with certainty so far does not exceed the limits of variation of heterozygotes.

If we leave aside the effect of provoking the excessive development of glumes in the ear, then we may consider as next important feature in "São Paulo Pod" corn the accentuation of female tendencies in the tassel and the reappearance of characters lost in the phylogeny of many grasses: the re-establishment of hermaphroditism in individual flowers and the occurrence of spikelets with more than two flowers. But this does not necessarily mean that the immediate wild ancestors had these characteristics and may thus have belonged to another group of grasses, not the Maydeae or Andropogoneae. We may have to deal with still older characteristics of primitive grasses.

Recently Mangelsdorf and Reeves have modified the theory that pod corn with its covered grains in the ears is an approximation to the wild ancestor of maize, assuming that this ancestor was a plant without the lateral ears, but with covered seeds in the tassel. If this would be true, we should expect that the lateral branches, instead of having still normal, but sterile ears, should also terminate in some sort of bearded tassel. Selection in this direction has been started, but in order to obtain positive results it seemed necessary to substitute the modifiers of cultivated corn by modifiers of a "wild" form. This seemed possible only by crossing pod corn to teosinte.

F. G. Brieger

C - Hybrids between teosinte and "São Paulo Corn" - Hybrids were produced between teosinte and heterozygous "São Paulo Pod" corn, consisting of tunicate and non-tunicate plants.

The tu plants in F_1 corresponded as a whole with the descriptions given by other authors, and we shall withhold discussion until the analysis of F_2 and backcrosses, now under way, are terminated.

The F_1 tunicate plants, however, showed many unexpected characteristics, some of which only will be mentioned here:

The Tu effect on the tassel was completely recessive-hypostatic and it was impossible to classify the F_1 plants as in the original "São Paulo Pod", according to the transformation of the tassel. Thus the tassels of Tu plants and their normal tu sisters were identical.

The ears, however, were very different in Tu and tu hybrids. In the latter the rows were mainly single, or when the paired row was not suppressed, they contained female spikelets only. Two paired rows appeared generally in

the Tu plants, one being an ordinary female spikelet, with one sterile and one female flower, while the other spikelet became pedicelled and contained two male flowers. Furthermore, there was a pronounced tendency to produce not only 2 double rows, but 3 or even 4.

The scales formed by the rachis and which cover more or less the grains in teosinte or in tu F_1 plants, were smaller and soft in Tu plants while the glumes became pointed.

The rachis and glumes of the tu hybrids are extremely horny, and it was very hard work to shell the seeds. On the other side, the rachis in Tu F_1 plants is extremely brittle and it was nearly impossible to harvest complete mature ears, since they fell apart immediately after removing the shucks.

Thus the Tu gene has a very different phenotypic effect in pure corn and in teosinte-corn hybrids. In the former we observe a pronounced tendency to introduce femaleness into the tassel, while in the latter maleness appears in the ears, or better on the lateral branches. A selection experiment is under way with the end of fixing this condition, just as it was possible to fix more or less the bearded tassel.

The fact that the Tu-gene acts in nearly opposite directions according to the modifier complex present, should warn us not to draw premature conclusions on gene action. The appearance of covered kernels is a universal effect of the Tu gene, while everything else depends upon the modifier back-ground. The Tu F_1 plants described above seem to me much more likely to be a replica of an ancestral wild grass than the Tu corn plants with bearded tassel, especially considering the following points: a) the rachis is extremely brittle: b) the lateral branches are not suppressed, but grow perfectly normally, producing terminally a tassel or an ear, and laterally still more branches or higher order with a varying number of additional ears: c) instead of a reduced or sterile ear, we encounter ears, where one female spikelet tends to be associated with a male spikelet.

While I think that the general structure of the Pod-Corn-Teosinte hybrid is a more likely reproduction of a hypothetical wild ancestor of corn as compared with the bearded Pod Corn, I do not believe that this ancestor actually was a hybrid.

There have been proposed several hypotheses to explain the morphological nature of the many ranked corn ear. Here again our Pod-Corn-Teosinte hybrids offer valuable material since the paired spikelets are often different, one being sessile and the other pedicelled. In two-ranked ears or in tassel branches we find in general a very regular situation. Both sessile spikelets are localized near the ventral side of each alveolus and the pedicelled spikelets on the dorsal side. But this symmetry seems to be the consequence of some physiological conditions. In many-ranked ears I did not find a regular position of two spikelets of the alveoli of each double row. The sessile spikelet may be on the left or on the right side of the pedicelled spikelet.

Other interesting observations could be made in some of the F_2 plants. In several instances, an alveolus contained one sessile spikelet

and one "branch" which carried one spikelet more or less in the middle and another at the end. If the pedicel was shortened three spikelets appeared close together in the alveolus. In one instance an alveolus contained 4 spikelets which probably were derived from two reduced branches with 2 spikelets each.

Finally all observations seem to indicate that the only constant orientation of the alveolus may be the longitudinal row, sometimes obscured by a twisting of the rachis, or altered by the intercalation of new double rows. The appearance of 3 rows of alveoli, the transition of this arrangement into one with either 2, by suppression, or of 4 double rows, by intercalation, is quite frequent. The alveoli may be all at different levels, or at the same level. Neither yoking nor a spiral arrangement could be observed with any regularity.

Thus the Tu F_1 and F_2 plants offer very interesting material, especially when studied at flowering time and not when their ears have become hard and mature. There cannot be any doubt that this material will finally permit a critical discussion of the hypothesis of the nature of the ear and the formulation of a new, combined theory, containing to some extent elements of older views. But the final discussion will be delayed until the analysis of the mature F_2 and backcross ears is completed.

F. G. Brieger

D - A histological study was carried out on several strains of native and cultivated corn and of a North-American pop corn. The structure of the latter was identical with that described by Randolph. In corn of the Paraguay river group, as defined above, the following structural elements were the most striking:

The spikelets appear to have a pronounced pedicel.

At the lower base of the pedicel and at its sides a scaly outgrowth of the rachis appears which thus surrounds the alveolus on three sides, and which corresponds to the cover of the kernels in Tripsacum and Euchlaena.

The spikelets of Paraguayan corn which when mature had the kernels half covered by glumes, had at flowering time the same structure as "São Paulo Pod" corn with well developed glumes.

F. G. Brieger and H. C. Cutler

E. Tripsacum australis:

Seeds and rootstocks of this species collected by Cutler were planted. Only two seedlings germinated and grew slowly. One of the rootstocks gave a large plant which started to flower in November and is still in bloom. The second is starting now in January.

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It has 18 normal pairs at meiosis.

E. A. Graner

3. Genetics of Aleurone Color

It is generally accepted that the presence of anthocyanin in the aleurone is due to the presence of certain alleles of the locus: A1 - A2 - C - R. But, as I have pointed out elsewhere, the action of the genes at these four main loci is conditioned by the coordinate action of the modifier complex. This could be shown by several selection experiments.

A line of red brittle, originally from Cornell, served to demonstrate that by selection, completely colorless ears may be obtained. In the original line occasionally a colorless grain occurred, and it was possible, by selection for higher number of colorless grains and for paler color of the still colored ones, to extract a line which was completely colorless. When backcrossing to colored lines, no clear segregation could be obtained.

Some of the brittle kernels of the original line appeared to be nearly black, which was attributed to the effect of an intensifier absolutely linked with bt, or to the action of the respective bt allele itself. All selection against this factor was useless. In the extracted colorless lines there still appeared a segregation for a recessive gene, producing deep black brittle kernels. Thus a gene which in the original material was only an intensifier and as such difficult to analyze and classify, became in the extracted lines a recessive determiner of anthocyanin color.

Since no crossing over has been observed so far, we suppose that the original line contained two alleles of bt: the ordinary bt without effect on aleurone color and the new allele bt^r which causes a deep black color and which is epistatic, when homozygous, over the modifier complex which dominates otherwise the action of ACR. In formulas, we represent the situation:

bt	bt	A1	A2	C	R	+ original modifier group	= purple (Pr) or red (pr pr)
bt ^r	bt ^r	A1	A2	C	R	+ " "	= black (Pr or pr pr)
<hr/>							
bt	bt	A1	A2	C	R	+ extracted modifier group	= colorless
bt ^r	bt ^r	A1	A2	C	R	+ " "	= black

The opposite result was obtained in "Chavantes" which as mentioned above has probably the constitution: A1 A2 Cⁱ R where Cⁱ represents a dominant inhibitor at the C locus. Pale purple (Pr) or red (pr pr) kernels occurred in the original material and, by selection, ears could first be extracted which segregated colored kernels in various proportions until finally fully colored ears appeared.

A corresponding situation was found in "Diamantino III" where a sharp segregation occurred for black or orange kernels. But black grains gave ears which segregated for a recessive orange while orange kernels gave ears segregating for a recessive black. The classification was generally

easy, but the ratio colored : colorless did not correspond to any standard Mendelian ratio.

It is remarkable that some lines segregate normally in some crosses, and show the modifier effect in others. Thus a "Golden Bantam", when crossed to a cc sh sh - test line was shown to be AA CC rr giving a 9:7 ratio in F₂, but crossed with the red-brittle line a mono-factorial segregation was obtained only in part of the offspring and a selection for both low and high ratios of colorless was successfully carried out.

These results may be summarized in the following form:

There are some lines where the modifier complex is well established and in balance with the determiners, not interfering with their action. Such lines give sharp segregations with normal Mendelian ratios.

Other lines have an unbalanced modifier complex and here selection experiments may give positive results. Thus it was possible to shift the color from red to white in the red-brittle line and from white to purple or red in "Chavantes".

The experiments are being continued and it is hoped that eventually a more complete understanding of the physiological action and interaction of determiners and modifiers may be obtained.

The selection line of "Chavantes" was very instructive in showing that we must distinguish between modifiers which act as plant characters and others which are evidently only aleurone characters. It may at first seem strange that aleurone characters may be dependent upon genes of the mother plant, and not only upon their own genes. However the effect of plant genes upon the endosperm seems to be quite general. The difference between flint and dent, between round or pointed kernel, to a large extent the difference between flint and floury, are inherited as a plant character. Now, if sporophytic genes control the type and distribution of starch in the kernel, there is no reason why one should not accept the same for the formation of anthocyanin.

F.G. Brieger and George O'Neill Addison

4. Yellow-orange Endosperm

Studies on the genetics of the yellow-orange endosperm started at Piracicaba, Brazil, (1937), were continued at Columbia, Missouri, in 1942, through the help of a fellowship from the Guggenheim Foundation.

A deep orange endosperm from Brazil (commercial strain) was used and crossed with several white endosperm strains. These crosses gave only segregation for one pair of factors. Some were continued until F₄ and the white endosperm strains checked proved to be yl yl Y3 Y3. Crosses with some white endosperm testers segregated again 3 colored : 1 colorless and showed independent assortment for chromosome 2 (lg 1), 4 (su 1) and 9 (df 3) indicating that the yellow gene segregating should be the Y1 in chromosome 6.

The same deep orange strain when crossed with a tester received from Dr. Jose Ma. Andres, Argentine and called A-(alal B-) (Pl-yl yl) showed a clear segregation of 9 orange : 3 yellow : 4 white. The numbers of 3 ears

taken at random are the following:

No. of the ear	Orange	Yellow	White	Total
40 - 12D \pm 1942	156	42	61	259
31 - 12D \pm 1942	154	56	62	272
Sib 49 x 17 12D 1942	137	43	49	229
<hr/>				
Total	447	141	172	760

Linkage was found with the P1 gene (repulsion phase) and all yellow seeds were albescent al, the white ones segregating 3 Al: 1 al. As the al gene is probably the same as y3 or very closely linked to it, it could be said that the deep orange Brazilian strain has both Y1 and Y3. The linkage with chromosome 2 in this cross was also shown by the segregation of B. The al strain when crossed with lgl showed absolute linkage (repulsion phase). By the segregation of A it was found that chromosome 3 was not involved.

The 9 : 3 : 4 instead of a 9 : 7 ratio as found by Perry and Sprague (1936) seems to indicate the existence of another complementary gene, probably to Y1, which probably is a plant character, since its segregation was not shown in the F_2 seeds. The F_2 plants are now growing, but have not flowered to this moment.

The F_1 of the same cross was used at Columbia, Missouri, for crossing with other Y-testers, received from Dr. H. S. Perry and the plants are growing at Piracicaba. Some unexpected ratios, were found in these crosses and will be checked in the next generation.

The deep orange Brazilian strain planted at Columbia did not flower there. So this strain could not be crossed with other testers. However, it was possible to use an Argentine strain called Colorado Casilda and belonging to Dr. L. J. Stadler's collection. This strain has practically the same color as that of the Brazilian one and its name indicates the same variety used by Dr. J. Ma. Andres in Argentine (1939) and giving results similar to those reported here. This Argentine variety will be now crossed to the orange Brazilian strain, but to save time, it has been crossed to testers for all chromosomes. The collection of testers used was prepared at Columbia, Missouri, and includes material from Cornell (Coop) and from other corn geneticists of the States. These crosses are being checked now at Piracicaba, Brazil, where the plants are just flowering, but the situation is rather complicated since we do not know the background of the testers used with respect to the Y genes. Also, it should not be expected that we have to deal with only one sporophytic gene but several may be acting as modifiers, giving the shades found in different yellow-orange endosperm strains.

Other strains of yellow-orange corn of different origin are also being tested. Some pop-corn ears from Brazilian material showed segregation approximately of 3 white : 1 yellow-orange, and we don't know if we have here to deal with a new Y factor or only with an inhibitor of the known Y genes.

Seeds of Y4 and It received from Dr. W. R. Singleton proved to be identical with Y1 and Y3, respectively. I think also the Y2 of Dr. W. Eyster in chromosome 5 is the same as Y1; so, the general situation of the yellow-orange endosperm for the present could be simplified with only the Y1 and Y3 as complementary factors and one or more plant-character genes modifying its shade or being complementary to them. Besides this should be kept in mind, the possibility of the existence of other seed genes for yellow endosperm color, as reported by Dr. G. F. Sprague (1938).

E. A. Graner

5. Yellow Aleurone

In the crosses with deep orange endosperm of Brazilian strains and white ones, segregation of a yellow-aleurone gene was found. The interaction of this gene is very variable and in some back-grounds difficult to classify. Also, the dosage in the endosperm makes the problem difficult since it was found that "simple" is not different from "nuliplex" white seeds when the yellow-aleurone strain is used as male parent. Until now it is possible to say that this gene did not show linkage with chromosome 2, 3, 5 and 6. Thus, it is not the Bn2 reported by Dr. G. F. Sprague (1934). It has now been crossed with the Bn1 in chromosome 7 and with testers for the remaining chromosomes. The gene gives, in some cases with the yellow-orange endosperm, a segregation of 12 orange : 3 yellow-aleurone : 1 white or 15 colored : 1 colorless.

E. A. Graner

6. Linkage Tests

A small number of linkage testers, of Cornell origin, was brought over from England and some others from Cornell. It was soon evident that these North-American strains are difficult to grow in Brazil. They were all rather small and weak, so that it was necessary to plant them in especially prepared beds. They seem to grow and produce reasonably well when planted in the first part of summer, that is, during the period when the length of the day is still increasing. For crossing purposes, it was always advisable to make several successive plantings, with the hope that sometimes the flowering period of the strains to be crossed may coincide.

Crosses between these imported lines and local lines, such as Cateto, or with native Indian corn (Diamantino III) Chavantes, etc.) were carried out and the extracts from these hybrids, are promising.

F. G. Brieger

A good collection of recessive and dominant genes in all chromosomes was organized at Columbia, Missouri with material received from Cornell (Coop) and from Drs. L. J. Stadler, H. Roman, L. F. Randolph, H. S. Perry, C. R. Burnham, R. A. Brink, W. R. Singleton and others. The plants are now growing at Piracicaba, Brazil, and they are growing very reasonably. After some experience we think it possible to grow in Brazil some of the American strains in the months of November to January, when we have the maximum of light, about 15 hours a day. Plants sown in December are flowering in 50 days as compared with the same strains in Columbia, Missouri, flowering in 55 days.

The problem of genetical tests for Brazil consists in the transference of the genes to late Brazilian strains, but we don't think this solution satisfactory since some segregating plants will be so late as to make our work difficult.

The principal genes in all chromosomes were crossed in Columbia with an Argentine strain and the hybrids look good for our conditions. We think it will be possible to isolate the segregating genes in this background and in plants not too late and promising for Piracicaba.

Deficiency testers produced by X-ray in chromosomes 3, 4, 5, 6, 9 and 10 were introduced into our collection from material of Dr. L. J. Stadler. The deficiency in chromosome 5 is linked with Pr, in chromosome 6 with Yl and in chromosome 9 with I. The deficiencies in chromosome 3, 4, and 10 were crossed respectively with Rg, Tu and Og in order to get these dominant genes linked with them.

Translocation-B testers from Dr. H. Roman for chromosomes 1, 4, and 7 were also brought to Brazil. The Tb-4 test has been useful in checking the su gene in many of our experiments.

A collection of trisomics from Cornell will be crossed with the respective recessives in order to facilitate its conservation without the necessity of cytological work.

The use of all these tests was started at Columbia, Missouri, in checking new mutants and will be continued at Piracicaba, Brazil.

E. A. Graner

7. Brazilian Stock Treated by Ultra-violet

A Brazilian hybrid corn that flowered normally at Columbia, Missouri, was treated by ultra-violet. Pollen grains were treated and used for pollinating untreated plants. The 600 seeds collected from 3 ears were sown in Brazil, giving good germination (80%). The plants are growing and the mutants in this background, proper for Piracicaba, will be used as testers after their localization in their respective chromosomes.

E. A. Graner

November 22, 1943

To Maize Geneticists:

In the Indian Journal of Genetics and Plant Breeding (2: 184-186. 1942) is a review by B. S. Kadam entitled: Maize Genetic Cooperation News Letter No. 16. 1942. The review of this News Letter seems to me to have been fairly well done. The point at issue is that no request was made for permission to publish such a review. News Letter No. 16 included this statement:

"The presentation of data in these news letters is not to be regarded as constituting publication. These data should not, therefore, be used in published papers without the consent of the authors."

The above statement was quoted in connection with the review and no data were published in the review. It includes only summary statements about the reports contained in the News Letter. It is evident, therefore, that Kadam obeyed the letter of the quoted injunction. I cannot, therefore, do what I was at first inclined to do, namely, to notify him that his name would be removed from our mailing list.

We have for years sent the News Letter on request to numerous workers in other fields of genetics. The principal objection that I see to such use as Kadam has made of these Letters is the confusion that may come from it. The Letters are not available in the libraries of the world. Such reviews as that published by Kadam are apt to bring numerous requests for the originals. Perhaps Cook was not far wrong in his objection to such "unpublished publications". The question that I wish you would answer for me is: should we send the News Letters only to workers in maize genetics? Please give me your opinion.

Sincerely,

RAE:P

R. A. Emerson

This is being sent to -

E. G. Anderson
R. A. Brink
C. R. Burnham
H. K. Hayes
M. T. Jenkins
D. F. Jones
E. W. Lindstrom

Barbara McClintock
P. C. Mangelsdorf
L. F. Randolph
M. M. Rhoades
G. F. Sprague
L. J. Stadler

MAIZE GENETICS COOPERATION

NEWS LETTER

18

January 31, 1944

The data presented here are not to be used in
publications without the consent of the authors.

Department of Plant Breeding
Cornell University
Ithaca, N. Y.

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I. IMPORTANT NOTICE

The Maize Genetic Coöperation News Letters carry a statement to the effect that the presentation of data in them is not regarded as constituting publication and that no such data are to be used in publications without the consent of the authors. A foreign geneticist and plant breeder, not working with maize, has published a review of News Letter 16, 1942. He was aware of the injunction and quoted it in the review. He included none of the data but did include the perhaps tentative conclusions drawn from the data by the authors. While, therefore, he obeyed the letter of the injunction, it can hardly be maintained that he accepted the spirit of the rule.

I conferred by letter with a number of the more active coöperators in this country. Replies ranged from one extreme to the other. Some thought that even such publication as had occurred might be disastrous and that, in the future, the News Letter should be sent only to those coöperators who contributed material. Others saw little danger, at this stage of our work, from such a review as had been published and suggested no change other than a rewording of the injunction. Most replies suggested a middle course between these extremes. I am, therefore, adopting the following procedure. This News Letter is being sent to those who are now coöperating or who have furnished material in the not too distant past. Further copies will be held here to be sent on request to other geneticists or breeders. I shall have to depend on my own judgment (good or bad) in determining whether particular requests shall be honored.

R. A. Emerson

II. FOREWORD (Swan Song)

I have been connected more or less intimately with Maize Genetic Coöperation from its beginning. Some years I have had to devote considerable time to it and other years almost none. On the whole I feel that I have probably done less than I should and certainly less than I am credited with having done. I am now an "emeritus" and rather enjoy it. I am anxious to complete (before my number comes up) certain maize genetic problems that have been underway for a long time and which will require yet further years of work. I am willing to admit no more than that I am not growing younger as the years go by. Any way I feel that, whether well or poorly, I have about done my stint and that some one else should soon assume responsibility for this coöperative effort. An appropriate time for a change is now when our most recent grant from the Rockefeller Foundation is to be closed out.

I shall, of course, retain an interest in this undertaking. If no other prior arrangement is made, I shall probably find myself planting certain genetic stocks again next spring and at pollination time shall wonder why I haven't yet learned to limit my planting to what I can take care of.

During the past year, many genetic stocks that were most in need of replenishment were grown and pollinated by Dr. M. J. Murray and Miss Rosalind Morris. Miss Morris has grown in the greenhouse many cultures showing seedling characters. When resort must be had to ears from normal plants of segregating cultures, it is important to determine which of the normals are heterozygous for the characters in question. Dr. Murray also spent much time in a study of the stocks on hand and of the available records and succeeded in bringing at least some measure of order into the rather chaotic situation that I had allowed to develop.

R. A. Emerson

III. REPORTS FROM COÖPERATORS

Bureau of Plant Industry Station, Beltsville, Maryland

A cross involving opaque-2 made in 1942 and selfed in 1943 segregated for an endosperm-color gene very closely linked with opaque. The gene has not been identified but since no gene affecting endosperm color previously has been reported in this region of Chromosome 7, the preliminary data are presented in the following table:

<u>Flinty</u>		<u>Opaque-2</u>		Total
Dark Yellow	Lemon Yellow	Dark Yellow	Lemon Yellow	
2337	21	42	752	3152

The data are not too satisfactory as considerable difficulty was experienced in classifying the opaque seeds for color. They indicate about 2 percent crossing over between the two loci. No symbol is suggested for the endosperm-color gene as too little information is available on it at the present time.

Merle T. Jenkins

Bureau of Plant Industry and Purdue University
Department of Botany, Lafayette, Indiana

In 1941 one plant from a very uniform appearing ear-row of inbred Kys produced a self-pollinated ear segregating approximately 3:1 for salmon yellow and ivory colored kernels. When planted in a germinating bed the yellow seeds produced all green seedlings and the white seeds produced only albinos. In 1942 a row was grown from the yellow segregates and each plant self-pollinated. Of the 20 ears produced, 7 were homozygous yellow and 13 were segregating for yellow and white. Seedlings grown from these segregating ears gave the following totals:

	: Seeds :	Seedlings	
	:planted:	green :	white
Yellow seeds:	3910 :	3030 :	14
White seeds :	1104 :	11 :	785

Ten of the 11 exceptional green seedlings from white seeds were successfully transplanted and grown to maturity. Because of unfavorable conditions only five of the attempted self-pollinations were successful, but in every case both yellow and white kernels were produced. It appears probable that a single gene with a dual effect was involved in the original mutation, and that the aberrant seedling types were due to hetero-fertilization.

A. M. Brunson

Columbia University, Department of Botany, New York City

1. In a stock homozygous for the dominant Bt-1 allele a mutation occurred from Bt to bt^m. This new allele is unstable and mutates with a high frequency to Bt. Seeds of bt^m bt^m constitution are mosaics of normal and brittle tissue. Germinal mutations are numerous - 7.5% of the seeds on selfed bt^m bt^m plants are reverse mutations. The Bt alleles obtained by reverse mutation are stable. The bt^m allele occasionally mutates to a stable bt allele which is indistinguishable from the old bt allele. While genic modifiers influencing the mutability of the bt^m allele exist it is evident that this allele is intrinsically unstable, and this case is not similar to the a Dt situation.

2. Goldschmidt in the Proc. Nat. Acad. Sci. 1943 reports a situation in *Drosophila melanogaster* where the interaction of alleles at two different loci gives results somewhat similar to those reported for unstable genes. He suggests that the idea of unstable genes be abandoned, and that the so-called unstable genes of *Drosophila* and maize can be accounted for in terms of factor interaction, epistasis, and threshold conditions. He specifically cites the a-Dt case in maize. According to his interpretation the apparent mutations of a to A, believed to be induced by the Dt gene, are in reality cases where a new Dt allele (which will be represented Dt^A) produces the color ascribed to the A allele. He also states that no published data exist which negate his interpretation. Actually two decisive experiments have been published which establish the correctness of the mutation hypothesis. (1) The A alleles obtained by mutation from recessive a show the expected linkages with genes in chromosome 3. On Goldschmidt's scheme the color-producing allele would be in chromosome 9 since Dt is in that chromosome. (2) When a mutation of a to A occurs in a cell of a a Dt Dt constitution the constitution of that cell following mutation is A a Dt Dt. On Goldschmidt's scheme it should be a a Dt^A Dt.

M. M. Rhoades

3. The vascular bundles of corn leaves are surrounded by a single layer of bundle sheath cells possessing plastids differing in size and shape from the chloroplasts of the mesophyll cells. The plastids of the

mesophyll cells contain no starch; the sugars they produce are moved into the bundle sheath cells and there transformed to starch. Starch increasingly accumulates in the bundle sheath plastids in the day; during the night the starch is changed to soluble carbohydrates and translocation occurs. The plastids of the bundle sheath cells are usually devoid of starch by morning. These plastids contain a green pigment, presumably chlorophyll, but are of a lighter green color than are the chloroplasts of the mesophyll. Photosynthesis may occur in the bundle sheath plastids. However, the green color of the bundle sheath plastid is similar to that of the guard cells of the stomata. Sayre found that the guard cells of *Rumex* contained a light green pigment which was not chlorophyll. In view of the above facts it will be of interest to ascertain whether or not the green pigment in the bundle sheath plastids is chlorophyll.

Each of the bundle sheath plastids contains numerous, discrete regions, which may be likened to pyrenoids, in which the starch is deposited. It is surprising that the structure and functions of these unusual plastids have not been adequately described. Kiesselbach (1916 and cited in Weatherwax 1923) noted their abnormal size and shape but did not mention their function in starch synthesis. He believed these plastids had different shapes in fixed from those in living material. We have observed, however, the same variation in size and shape in both fixed and living cells.

M. M. Rhoades and Alcides Carvalho

Connecticut Agricultural Experiment Station
New Haven, Connecticut

1. Long-inbred lines of corn infrequently show heritable variations. A search among all the inbred material available over a period of several years has revealed deviating lines that differ from the original type in some distinct morphological or physiological character. Presumably these variations are single point mutations, although it is difficult to separate primary changes from delayed segregations. All variations so far found appear to be degenerative changes, reducing the ability of the plant to grow and to reproduce itself. They include delayed flowering, leaf blotching, narrow leaf, reduced plant size at maturity, crooked stalk and chlorophyll alterations.

All of these have occurred naturally. In X-rayed material less conspicuous variations have been found but these are not sufficiently well marked to segregate clearly.

Four of the natural variations have been crossed back with the normal lines from which they come. All have given the surprising result of a hybrid-vigor effect. The F_1 plants are either taller, greener, broader in leaf and stalk, earlier in flowering or more productive of grain. The differences are small but measurable. If it is proved that these differences involve only a single gene this would be clear evidence that heterosis is something more than an accumulation of non-allelic dominant favorable growth factors.

It may also be questioned fairly whether these are actually the degenerate types that they seem. From evidence previously reported these reduced lines may give superior results in outcrosses. Since these mutations presumably originate in the heterozygous condition, the plants containing them should be more vigorous than the homozygous individuals in the same line and are likely to be selected for propagation. This was actually the case in the blotched leaf line that came originally from a plant selected as superior in height of stalk and ear development to the other plants in the same self-fertilized progeny. This is additional evidence to show why inbred lines are difficult to maintain in a constant and uniform condition.

It may also explain why some of the poorest lines are so useful in production of commercial hybrids. For example, Iowa L317, C.I. 540 and 4-8 are notably unsatisfactory as inbreds but are used in hybrids that are widely grown. Combining ability results from a complementary action that is not clearly indicated in the homozygous condition and apparently involves an equilibrium of genic material that is not as yet fully understood.

2. The reciprocal crosses reported last year, made between inbreds with extreme differences in kernel size (Rice pop and Reid dent) again showed significant differences in early growth. These differences almost entirely disappeared by flowering time. The combined average days to tasseling and silking were 81 for the pop inbred and 66 for the dent. The two reciprocal crosses were 66 and 65. The crossed plants from the larger seeds flowered one day earlier. Differences in tillering also went with the larger initial growth, where the seed was produced by the non-tillering parent. The average number of tillers this year is dent 0, dent x pop 2.7, pop x dent 2.1 and pop 2.9.

3. Plants grown in the greenhouse and transplanted to the field are sometimes shorter at maturity than plants grown from the same seed sown directly in the field. Very small, immature seeds from ears that are harvested at an early milk stage usually produce plants that grow to normal height and productiveness. This suggests that tall plants that are difficult to pollinate might temporarily be reduced in height advantageously. Possibly better means could be devised to do this, such as bending the plants to the ground in the early stages of growth and allowing them to grow upright. The basal part could be held down by covering with soil, fastening with a wire staple or tying to adjacent plants.

D. F. Jones

4. Considerable heterosis is manifest when Purdue 39 is crossed with Connecticut 30, a reduced type of P39. The P39.C30 hybrid in 1942 produced 25-30% more grain than P39. The hybrid also grew faster than either parent. The C30 type plant is recessive to P39 and the P39.C30 hybrid gives good monogenic ratios in both F₂ populations and in backcrosses to C30. C30 arose in 1933 in a selfed ear of the P39-16 stock of the Crookham Company, Caldwell, Idaho. Since there was no evidence of outcrossing it is assumed that C30 is a mutation. The interesting question is whether the heterosis found last year in the P39.C30 cross was produced by the same factor causing the C30 plant to be reduced or due to other factors that may have mutated since the C30 was separated from Purdue 39. Crosses made last year may give information on this point. C30 was crossed by several different sub lines of Purdue 39 maintained in different places and quite distinct in themselves. It will be interesting to see if as much hybrid vigor is obtained when P39-16 is crossed by C30 as when other more remotely related lines are crossed. The data on hand are insufficient to justify any conclusion regarding the nature of the hybrid vigor encountered in this intra-inbred hybrid. It could be explained by the

interaction of alleles, divergent in function as suggested by East. Further study is necessary to determine whether the factors responsible for heterosis are allelic or not. Whatever the explanation this phenomenon like hybrid vigor between different inbreds, may have its practical application before we understand fully the cause of the hybrid vigor. If the yield of Purdue 39 can be increased 25% or even 10% by first crossing with C30 it would seem logical for the seedsmen to use the C30.P39 hybrid in production fields wherever P39 is ordinarily used as the seed parent. Since it has been found that C30 hybrids are equal if not superior to P39 hybrids, seedsmen might well utilize the hybrid vigor of the P39.C30 hybrid in their seed fields to increase their seed yield without sacrificing in any way the quality of the finished hybrid.

5. Effect of C30 on the production of new mutants.

In the cross of P39 x C30 several cases of defective and germless seeds have been encountered. The number of segregating progenies has been small and consequently no rate has as yet been determined. It is our belief that a rate exceeding the normal mutation rate will be found when more data are accumulated. Besides germless and defective seeds, a virescent seedling was found to be segregating in a selfed progeny of the cross P39 x C30. No such virescents have been observed in either P39 or C30. The virescent when selfed produced 100% virescent seedlings. The inheritance of the new virescent will be determined. Also P39, C30 and the F_1 hybrid will be examined cytologically.

6. A light yellow factor or yellow reducer has been found in a stock of white sweet corn, Early Pearl. In changing Early Pearl from white to yellow this character was observed. Such yellow reducers are common in certain of the late white varieties of field corn grown in the south but are not frequently encountered in sweet corn. The ones we have always observed it in are Early Pearl, Sugarsweet or Cupid, and Hayes White. These varieties are similar and probably have a common origin. The new light yellow is dominant over the intermediate or darker yellow and in the F_2 gives a good ratio in most sweet corn crosses of 3 light yellow: 1 darker yellow. When backcrossed to the regular yellow a good 1:1 ratio of light: dark is obtained. If backcrossed to light yellow the kernels are all light. The light yellow condition is homozygous in one of our commercial inbreds C35, derived from the Yellow Pearl. At the eating stage of ears heterozygous for light yellow no segregation for the light yellow factor can be detected, the color being a good medium yellow. Apparently the color is reduced during the drying process.

7. "First" Maize Breeder had Crossing Plot at New Haven in 1836.

In the 1845 issue (Vol. 2, p28) of the Cultivator magazine occurs an interesting letter from Noyes Darling, a New Haven lawyer and judge, telling how he developed a variety of sweet corn. The full letter will be published shortly, probably in the Journal of Heredity. We enclose an excerpt giving his procedure the first year, 1836.

"1st year. I had a very early yellow corn, but quite diminutive in its growth - the stalks not over 3 feet in height, and the ears not over 4 inches in length. Late in the season I planted this in a patch of sweet or shriveled corn, then considerably grown. As soon as the tops or blossoms of the yellow corn protruded, they were cut off, in order that the early corn might be impregnated only by the sweet corn. The result this year was yellow corn of the usual size and appearance."

This then appears to be the first crossing plot in which one variety was detasseled to be pollinated by another although James Logan had cut tassels off of corn 100 years earlier in his experiments to determine whether pollen was necessary for fertilization. However Darling's experiment seems to be the first time a maize breeder had detasseled a variety of corn in order to make a controlled pollination. From the sweet-flint cross, by selection he produced

7.

an early white sweet corn that matured on July 18 in New Haven, a very early corn. He described his experiment in a concise, accurate fashion that would serve as a model for scientific reporting today.

W. Ralph Singleton

Cornell University, Department of Plant Breeding,
Ithaca, New York

Aberrant pericarp-color ratios. In last year's News Letter (17:8-10, 1943), I reported a disturbance of pericarp-color ratios unlike that caused by the recessive zygotic lethal, z1. Selfed red ears gave progenies with approximately equal numbers of red and of white eared plants instead of the expected 3-1 ratio. Such red eared plants, when used as pollen parents in crosses with white gave progenies with about four times as many whites as reds. Only part of the red ears of such cultures gave aberrant progenies. The possibility of this disturbance being transmitted thru the egg had not been determined.

More data of the same kind and a few new data are now available. The new and older data are summarized in the accompanying table.

Normal and aberrant pericarp and cob-color ratios

: Progeny:		: Progenies:		: Phenotypes and No.:		: Approx.:		Remarks
Line:	of line:	Parental	No. of	of individuals			ratios	
No.:	No.:	genotypes	cultures:	R-R	W-R	W-W		
:	:	♀ ♂	:	:	:	:	:	:
1:	-	W-R x R-R	2	26	:	:	:	:
:	:	:	:	:	:	:	:	:
2:	1	$\frac{W-R}{R-R}$ (x)	11	651	182	:	3:1	Normal
:	:	:	:	:	:	:	:	:
3:	1	" (x)	3	175	153	:	1:1	Aberrant
:	:	:	:	:	:	:	:	:
4:	1	W-W x $\frac{W-R}{R-R}$	9	402	391	:	1:1	Normal
:	:	:	:	:	:	:	:	:
5:	1	"	7	290	1125	:	1:4	Aberrant
:	:	:	:	:	:	:	:	:
6:	5	$\frac{W-W}{R-R}$ x W-W	6	197	-	199	1:1	Normal
:	:	:	:	:	:	:	:	:
7:	5	$\frac{W-W}{W-R}$ x W-W	8	:	225	203	1:1	Normal
:	:	:	:	:	:	:	:	:
8:	6	$\frac{R-R}{W-W}$ (x)	8	125	-	114	1:1	Aberrant
:	:	:	:	:	:	:	:	:
9:	7	$\frac{W-R}{W-W}$ (x)	6	-	140	40	3:1	Normal
:	:	:	:	:	:	:	:	:
10:	7	" (x)	1	-	14	11	1:1	Aberrant
:	:	:	:	:	:	:	:	:

The pollen parents of the two F_1 cultures shown in line 1 were from the same stocks of chromosome 1 markers, P br f an gs, both homozygous for red pericarp and red cob, R-R. The pistillate parents were from unrelated stocks with colorless pericarp and red cob, W-R. Of 14 F_2 cultures, 11 (line 2) showed normal 3:1 segregation and 3 (line 3) gave aberrant ratios approaching 1:1. Other F_1 R-R plants were backcrossed as pollen parents to stocks with colorless pericarp and white cobs, W-W. Of 16 such backcross cultures, 9 (line 4) gave

normal 1:1 ratios and 7 (line 5) gave aberrant ratios approaching 1:4. Six red eared plants (line 6) and eight red-cob whites (line 7) of the aberrant backcross cultures were again backcrossed this time as pistillate parents; and all gave normal 1:1 ratios. Eight red eared plants (line 8) from these normal second backcross cultures when selfed gave only aberrant cultures. Finally, six red-cob whites from the second backcross cultures (line 9) gave normal ratios on selfing and one (line 10) gave an apparently abnormal ratio.

In summary, it should be noted that red eared plants of aberrant cultures when selfed or used as pollen parents in backcrosses to white, transmit the disturbance to some but not to all cultures of the next generation. When used as pistillate parents in such backcrosses, no disturbance is shown in the following generation, but both red eared plants and red-cob whites of that normal generation give aberrant results when grown one further generation.

From all this, it is clear that the disturbing factor is carried by a part (presumably one-half) of the female gametes and by a part (materially less than half) of the functioning male gametes. In its adverse effect on the functioning of male gametes, it is similar to the Ga reported by Rhoades (News Letter 17:7, 1943). I am, therefore, assigning to it tentatively the symbol Ga₄.

Since there is evidence (tho slight) of crossing over between Ga₄ and the pericarp-color locus and of differential functioning of male gametes, these two variables can be evaluated by use of F₂ or backcross ratios only when adequate data are available for a third nearly gene. The percent of crossing over can be determined directly, however, from the ratios of aberrant to normal cultures from (1) F₃ from reds of aberrant F₂ cultures and (2) from progenies of reds and/or red-cob whites of backcross cultures where Ga ga reds are used as the pistillate parents of the backcrosses. In these cases, the ratios of aberrant to normal cultures should be quite independent of the percent of functioning Ga pollen.

Limits can be set for the two variables by use of F₂ and backcross ratios of red to white. Thus, the observed 53 percent red eared plants of F₂ might be accounted for by various combinations of the two variables with extremes from zero crossing over with 6% functioning Ga pollen to 6% crossing over with zero functioning Ga pollen. But the observed 27 percent red eared plants in backcross cultures indicate very different limits for the two variables, namely, from zero crossing over with 27% functioning Ga pollen to 20% crossing over with 12% functioning Ga pollen. Since the crossover percentage must be the same for the two types of cultures, one of three conclusions must follow, namely, (1) my hypothesis is wrong (2) my calculations are wholly inaccurate, or (3) pollen functioning is affected adversely much more when the pistils to which it is applied are heterozygous for Ga than when they carry only ga. If the latter is true, the gamete factor, Ga₄, may be regarded as dominant as is Gal.

R. A. Emerson

Cornell University, Department of Plant Breeding, Ithaca, N. Y.
and University of Georgia
Department of Plant Pathology & Plant Breeding, Athens, Georgia

Chromosome 1.

Cross $\frac{Ts_3}{+} \frac{+}{Kn}$ x inbred ($ts_3 kn$)				
$Ts_3 +$	$Ts_3 Kn$	$++$	$+ Kn$	Total
78	2	5	68	153

% recombination = 4.6

Chromosome 2. Tetraploids

In the course of his intensive work on tetraploids, L. F. Randolph created a stock containing the genes lg, gl, b, v and a corresponding stock containing the dominants. Both stocks were homozygous A_1, A_2, A_3 and also R_8 which is necessary for definite classification of the genes B-b in the seedling stage. The stocks were multiplied and then selected for distinct expression of the four marker genes. Following this, J. E. Welch studied the linkage relations of plants duplex for each of the four genes when backcrossed to the multiple recessive. Beginning at this advanced point, I can contribute some additional information.

The cross of a plant duplex for all four markers

lg gl b v

lg gl b v

by a multiple recessive one lg gl b v should give as a parental

lg gl b v

class ratio four plants simplex for all genes lg gl b v to one

lg gl b v

plant duplex for all genes lg gl b v to one multiple recessive

lg gl b v

plant lg gl b v . Numerous other arrangements are possible in plants
lg gl b v
lg gl b v

derived from crossover gametes; but for any one gene, the individual plant should have the recessive allele represented either two, three or four times. The last type is obvious phenotypically since it is homozygous for a recessive marker. Further, a cross of this nature should and did segregate in the ratio of 3.6 - 5 dominants : 1 recessive for each of the four genes.

If several individuals with dominant phenotype are selected from such a backcross progeny, and again backcrossed to the multiple recessive, one should find that certain of their progenies give simplex ratios for all four gene members.

Twenty individuals were tested; their distribution is as follows:

- 2 duplex ratios for all four genes
- 1 duplex ratios for lg, gl and b; simplex ratio for v
- 1 duplex ratios for gl, b, and v; simplex ratio for lg
- 1 duplex ratios for lg and v; simplex ratio for gl and b
- 4 duplex ratio for v; simplex ratios for lg, gl and b
- 2 duplex ratio for lg; simplex ratios for gl, b and v
- 9 simplex ratios for all four genes

The study of progenies, derived from backcrossing plants simplex for each gene to the multiple recessive stock, should give the most direct measure of recombination frequency in a tetraploid for comparison with those in similar diploid stocks.

While 4,315 mature plants were studied, obviously only part of these may be used in the calculation of recombination frequencies from simplex ratios for any given region. The data are tabulated as a three-point test for lg, gl and b and as a two-point test for b and v. This enables one to utilize larger numbers than would be possible in a 4-point tabulation. No records were used unless the ratio of dominant to recessive allele was a good fit for a 1:1 ratio. In this manner, any possible effects of either differential viability or poor expression are kept at a minimum. Note that the total is smaller for the 2-point test as a number of cultures were not usable since the v_4 class was deficient.

0	(+ + +	1033	0	(+ +	484
	(lg gl b	1036		(b v_4	427
1	(+ gl b	196	1	(+ v_4	352
	(lg + +	192		(b +	359
					1622
2	(+ + b	181			
	(lg gl +	219			
				786 b : 836 + D/P.E. = 1.9	
				779 v_4 : 843 + D/P.E. = 2.4	
1 & 2	(+ gl +	55		1500 lg : 1466 + D/P.E. = 0.9	
	(lg + +	54		1506 gl : 1460 + D/P.E. = 1.3	
		2966		1467 b : 1499 + D/P.E. = 1.0	

The diploid recombination values used in the following table are taken from Fraser, Jour. Hered. 30: 375-378, 1939.

	4n	2n	Difference
lg - gl	16.8±0.46	19.5±0.40	2.7±0.61
gl - b	17.2±0.47	21.6±0.41	4.4±0.62
b - v_4	43.8±0.83	33.2±0.47	10.6±0.95

The observed differences between 2n and 4n are significant, but a discussion of the possible causes is too lengthy for this preliminary report.

Chromosome 7.

Certain stocks of the late Professor A. C. Fraser, and several of the co-op stocks as well, contain a factor for defective seeds. This recessive factor reduces seed size to $1/16 - 1/4$ that of normal and is somewhat variable in expression. Defective seeds entirely fail to germinate in weak lines but may produce $1/4 - 1/8$ sized plants in vigorous stocks. As a new defective seed mutant, this one would hardly command any attention. However, this semi-lethal was isolated by selfing cultures containing the genes in v_5 ra gl and these same cultures had previously shown unequal parental and crossover classes in 3 point tests. One may presume that this semi-lethal is linked rather closely with these markers and is the cause of these aberrant ratios. It is unlikely that this recessive by itself can account for the marked differences obtained in linkage results in different lines, unless it has an effect on crossing over when present in the heterozygous condition. This has not been studied. One might easily ascribe ears segregating for this gene to the effects of poor pollination, but ears segregating approximately 3:1 have been recovered from normal seeds taken from a segregating ear.

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Quantitative characters and dominance

Use of third degree statistics with this problem has been illustrated by Fisher, Immer, and Tedin (Genetics 17:107, 1932).

The less powerful but more ready attack with means does not require so extensive nor intricate data. Essentially the method is to test for departure from the additive scheme except for dominance by comparing F_2 mean with the mid-point of F_1 and parents, and backcross mean with mid-point of F_1 and parent. Some extension of the method is proposed and illustrated below.

Denote: n - number gene pairs heterozygous in cross; n_1 - plus pairs in parent farther from F_1 ; n_2 - pairs in near parent; $n_1 + n_2 = n$; α - aA effect minus aa effect; k - dominance factor, $(AA-aa)/(aA-aa)$; R - minimum phenotype summing effects of pairs aa or AA in both parents and aa effects of n pairs; FP - parent farther from F_1 ; NP - near parent; - etc.

For the additive scheme with pure parents;

$$FP = n_1 \alpha + n_1 k \alpha + R \quad (1)$$

$$NP = n_2 \alpha + n_2 k \alpha + R \quad (2)$$

$$F_1 = n \alpha + R \quad (3)$$

$$F_2 = 3/4 n \alpha + 1/4 n k \alpha + R \quad (4)$$

$$FB = 1/2 n \alpha + 1/2 (1 + k) n_1 \alpha + R \quad (5)$$

$$NB = 1/2 n \alpha + 1/2 (1 + k) n_2 \alpha + R \quad (6)$$

Eliminating R from (1) to (6) and combining n_1 and n_2 provides seven not entirely independent estimates of $(1-k) n\alpha$ and an eighth comparison $(2F_2-B) = 0$. Take: P - sum of parents; F - sum of F_1 and F_2 ; and B - sum of backcrosses. For Lindstrom's data on relative yields of three inbred lines of maize and their hybrids (Proc. 7th. Int. Gen. Cong.):

	$(1-k) n\alpha$	d
$4(F_1 - F_2)$	$= 136.8\% F_1$	15.1
$4/3(F-P)$	124.5	2.8
$2(B-P)$	142.0	20.3
$(2F_1-P)$	127.6	5.9
$2(2F_2-P)$	118.4	-3.3
$4(F-B)$	89.6	-32.1
$2(2F_1-B)$	113.2	-8.5
Mean	121.7	$(2F_2-B) = 11.8$; should be 0.

Lindstrom's data probably are a fair representation of the usual result - see Neal, J. Am. Soc. Agron. 27: 666.

The seven estimates of $(1-k) n\alpha$ are expected to be homogeneous and $(2F_2 = B)$ on the additive scheme, with no restrictions as to linkage, or as to degree, direction or other variation of dominance, or variation of Alpha.

In the event of no significant departure from the additive scheme the mean estimate of $(1-k) n\alpha$ may be of value to the breeder without further resolution into its factors. The quantity $(1+k) n\alpha$ or $(n\alpha + nk\alpha)$ estimates total range of genetic variation for the specific cross with free assortment. Distance from the lower extremity to F_1 is $n\alpha$; from F_1 to upper extremity is $nk\alpha$. The two are equal with no dominance. With dominance their difference is $(1-k) n\alpha$. Total depression by inbreeding is $1/2 (1-k) n\alpha$; depression from F_1 to F_2 is $1/4 (1-k) n\alpha$.

Taking the present case as additive, $k = (-121.7/n\alpha) + 1$. Then, $n\alpha$ must be as great as 121.7% F_1 if the conclusion of negative k is to be avoided. The factor k varies from unity for no dominance, through zero for complete dominance to negative values for over-dominance, "super-dominance," or "diverse alleles". With the conclusion of "complete" dominance ($k = 0$) $n\alpha$ must be taken 121.7 and the minimum phenotype minus 21.7. Taking the minimum at zero, $n\alpha$ is 100% and k is minus 21.7. The correct explanation of heterosis for yield in maize may lie somewhere between these somewhat arbitrary limits, involving both negative R and negative k. Note that on the additive scheme F_1 will not exceed the sum of parents without negative R or negative k, yet most maize inbred yields are less than one-half of F_1 yield. If k be negative, selection for increased

inbred yield will tend towards lower F_1 yield.

The obtained value of 121.7 places expected yield of a homozygote from these crosses at 39.2% F_1 , which is higher than usually obtained. The example may not be strictly additive. For further illustration of method, four of the seven estimates of $(1 - k) n\alpha$ involve $(-P)$ with average deviation plus 6.4, indicating that slightly higher inbred yields may be expected with the present hypothesis.

Cross of heterozygous maize varieties - Tuxpan x Golden Cross Bantam

	F_2		Backcross to G.C.B.		$(1-k)n\alpha$	S.D.	sk
	0	C*	0	C**		F_2	
Number leaves	13.7	13.9	12.0	11.6	+1.7	1.47	-3
Height, feet	7.5	7.3	5.4	5.9	+2.7	1.00	-2
Days to silking	73.9	70.9	66.6	65.2	-6.9	4.47	+3
Tassel length, ins.	17.4	16.6	14.6	14.7	+3.2	2.28	-1
Silking shoots	4.7	4.8	6.5	5.5	+2.8	2.30	+4
Ear diameter, cm.	4.4	4.6	4.2	4.3	+0.1	0.37	0
Cob diameter, cm.	2.5	2.5	2.3	2.3	-0.1	0.26	0
Husk length, cm.	24.0	24.6	21.1	22.8	-3.2	2.96	0
Ear length, cm.	19.1	19.6	18.1	18.6	+5.3	2.84	-1?
Husk extension, cm.	5.0	5.2	3.0	4.3	-8.0	3.33	+3
Number tillers	.9	.97	1.1	1.3	+0.9	0.91	+5
No. kernel rows	13.4	13.3	11.6	12.0	+0.4	2.27	+1

* Mid-point between F_1 and mean of parents.

** Mid-point between F_1 and Golden Cross Bantam.

sk Inspection grade of skewness: grade 5 as $1/2$ of a normal distribution.

Although these records are from heterozygous parents they show generally good agreement with the additive hypothesis. Interpretation for any character will involve first the comparison of F_2 and backcross means. Where agreement seems good, $(1 - k) n\alpha$ is next compared with skewness as to magnitude and direction. Finally, $(1 - k) n\alpha$ as a measure of dominance bias is considered with some measure of variation. Number of silking shoots and number of tillers have apparent skewness opposed in direction to the dominance bias. For tillers the explanation seems to lie in a piling up of nearly half of the frequency in the zero class; the character is not expressed to the left of or below zero. No explanation for silking shoots is apparent.

It is indicated that continued inbreeding would increase total husk length 1.6cm., while ear length would be shortened 2.6 cm. Husk extension would then increase about 4.0 cm. with inbreeding and decrease with crossbreeding of inbreds.

Powers (J. Agr. Res. 63: 161) presents records on plant height in centimeters for four tomato crosses. Mean estimates of $(1 - k) n\alpha$ are:

	<u>Danmark</u>	<u>Johannisfeur</u>
Red Currant	25.3	10.3
Johannisfeur	13.8, 7.1*	
Bonny Best		1.1

* Records for two years

The seven individual estimates on which each of the above is based do not show marked heterogeneity within any set in the writer's judgment. Variance of $(1 - k) n\alpha$ is apparently much greater between than within these crosses. Deviation from 0 of $(2F_2 - B)$ is slight in each case. The cross Johannisfeur x Bonny Best was discussed separately by Powers. He found departure of F_1 from mid-point of the parents not significant. F_1 and F_2 seem almost identical. Yet the seven estimates of $(1 - k) n\alpha$ are, 0.24, 1.31, 1.28, 1.04, 1.84, 1.36, 0.80; all positive, suggesting the expected mean may be some small positive value due to some degree of dominance bias, geometric interaction, or non-linear scale of environmental effects. Since $(2F_2 - B) = 0.28$, dominance may be the favored conclusion.

For the cross Danmark x Red Currant the far parent is 16.6 cm. from F_1 . Since $(1 - k) n\alpha = 25.3$ cm. the minimum phenotype, R, is 25.3 cm. farther from F_1 than is the maximum. It would appear that the far parent Red Currant has plus gene values not found in the other parent sufficient to explain the excess of F_1 over the taller parent. The writer sees no suggestion of negative k or negative R in the three crosses which have F_1 s taller than the taller parent.

Powers has noted that dominance bias may be affected by environment, which view is supported by the two records for separate years on one cross. Extensive analysis by higher order statistics, not being easily repeated, might be of doubtful value, if confined to one season or location.

There is of course, no new principle involved in the analysis by comparison of means suggested here. More efficient statistics for judging significance in some of the comparisons may be developed perhaps. If values of k, n, and alpha could be resolved by extensive analysis the quantity $(1 - k) n\alpha$ would still be of prime interest as a measure of dominance depression of efficiency of selection. Progress in breeding towards an objective involving several quantitative characters may sometimes be hastened by an efficient balancing of backcross and selection pressures. Those characters which have strong dominance depression away from the objective will be more difficult to recover from crosses by selection. Insofar as possible such characters should be collected in the recurrent parent, and thus largely recovered by backcrossing.

In the event of negative k (aA increment exceeds AA increment), regression of phenotype on number of plus genes (A) will rise to a point beyond which the mean effect of an (A - a) substitution is negative because of increasing homozygosity. From this point the F_2 distribution of

phenotype will be doubled back on itself with respect to gene number values. Analysis by comparison of means will not be distorted. Presumably, analysis by higher order statistics may also not be distorted but that must be investigated.

Analysis by comparison of means would seem to be a ready method where more extensive analyses cannot be employed or a reasonable preliminary to more powerful methods.

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Linkage relations of gl_4

$\frac{su\ Gl_4\ Tu}{Su\ gl_4\ tu} \times su\ gl_4\ tu$				
Su Gl_4 Tu	Su Gl_4 tu	Su gl_4 Tu	Su gl_4 tu	su Gl_4 Tu
20	3	9	33	18
su Gl_4 tu	su gl_4 Tu	su gl_4 tu		
7	1	6		
$\begin{array}{ccccccc} & & 30.9 & & & & \\ Su & & Gl_4 & & Tu & & \\ & 30.8 & & 20.6 & & & \\ \hline & & 43.3 & & & & \end{array}$				

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1. Midcob color. This character is difficult to study in this climate. Samples of the same inbred material were grown in 1941 and in 1942. In several cases a line that had red midcobs in 1941 was classified as having colorless ones in 1942. The ears in both cases were brought in at maturity and dried in the drier for final classification. 1942 was an unusually wet year, especially during August and September. Even under conditions where the ears matured and dried well in the field as in 1943, many ears classified in the field as having colorless midcobs were found to be colored after drying. Proper conditions for complete maturity and drying appear to be essential.

In 1943, apparent linkage was found between an interchange T5-6 and midcob color (30% recombination in 172 plants), indicating at least one midcob color factor may be in chromosome #5 or #6. A new factor for shrunken endosperm (sh_2), one of Stadler's x-ray mutants is linked with pr. Backcross data: 150 Pr Sh + 45 Pr sh + 51 pr Sh + 164 pr sh indicate 23.4% recombination. Its location in the chromosome has not been determined.

2. Dominant White Cap (W^C) appears to be in chromosome 1 based on the linkage observed with interchange 1-9c and the lack of linkage with 9-10a. Also there was no linkage with wx (using pollen classification for wx). Data with 1-9c (1942 and 1943): W^C = 80 semisteriles + 28 normals; yellow cap = 47 semisteriles + 74 normals or about 33% recombination. Dr. Hayes' earlier tests with bm2 were negative, while with gs there was a loose but significant linkage ($P = .05 - .02$). Such a linkage value would indicate W^C might be near br.

3. Zebra striped zb6. (Hayes, H. K. and Chang, M. S. Genetics 24: 60. 1939) was crossed with zbl, zb2, and zb3 and found to be genetically different from these three.

zbl is not in chromosome 6, as shown by a trisomic test (C. Lazaro)

4. Fasciated ear appears from my F_2 results to be a dominant character, not a recessive as listed in the Cornell Linkage Summary. (This stock is Coop. #39-25-6).

5. Crosses between interchanges involving the same two chromosomes.

T2-4a x 2-4c	=	semisterile F_1
T2-4a x 2-4b	=	"
T2-4b x 2-4c	=	"
T2-6c x 2-6d	=	20% sterility on ears, pollen also low
T2-9a x 2-9b	=	semisterile
T5-7a x 5-7c	=	29% sterility on ears (pollen also low)

The low sterility was thought to be the result of survival of a certain class of spores which ordinarily aborts. In crosses involving two interchanges in which the two breaks are close together and in the same relative position with respect to the spindle fiber (the same interchange having its break in each chromosome closer to the spindle fiber than does the other one) certain spore classes should be deficient for only one short region. According to the cytological data available, in T2-6c the breaks are in the long arms at .3 and .25 respectively from the S.F. in chromosomes 2 and 6; while in 2-6d they are also in the long arms but at .4 and .4. Deficiency tests for genetic loci in the two F_1 hybrids showing low sterility were all negative:

for T2-6c x 2-6d : ms, sl, pb were tested for chromosome 6
lg gl v4, ba2, ts were tested for chromosome 2.

T5-7a x 5-7c : bv gl6 for chromosome 5
sl, bd, gl, ra lj for chromosome 7

It seems probable that none of the genes tested is in the region suspected of being deficient.

C. R. Burnham

6. Red glume collar. Certain inbred lines and genetic stocks show a band of red color near the base of the glumes of the tassel. Most stocks are green at this point. The color may show only when the tassel is fully out of the boot, but it may show earlier. A few segregating progenies indicate

that in these cases the red differs from green by a single dominant factor. A backcross test involving this character and also Y and Pl indicates that red glume collar is closely linked with Pl (6.6% recombination), but the data did not indicate the probable order.

Another red glume collar character is found in B pl stocks, but in cultures segregating B-b, the collar color has always been associated with B.

C. Lazaro and C. R. Burnham.

Young tassels of both types b pl red collar and B pl red collar were wrapped up in black paper to exclude the light. In the first type (linked with Pl), the collar color developed in all cases in the absence of light. When the second type (associated with B) was bagged, the sun red color on the glumes did not develop, but the collar was colored, although not as intensely as that in the type linked with Pl. It appears, therefore, that the collar color is not a sun red color even in the type which is associated with B.

C. Lazaro

7. Trisomic tests with unlinked genes. Trisomic tests for chromosome 6 and the following genes were negative: zb, gl6, gl9 (trisomic plants had an excess of gl progeny as compared with the 2n), and v9. A seedling dwarf (one of Stadler's designated temporarily as ds-3) may be in chromosome 6 by this trisomic test.

Linkage data with other factors were obtained along with the tests for linkage in chromosome 6. The possible linkages are as follows:

Genes	N	Segregating for new characters	χ^2 for indep. test	Recom. \pm S.E.
pr - ws	104	3:1	P = .02	35.5 \pm 6.1
W ^c - si? [*]	164	15:1	P = .02	
Y - gl-11	283	3:1	P = < .01	38.5 \pm 3.8
Y - w (in gl6 culture)	202	3:1	P = < .01	27.0 \pm 3.8
Fl - gls-3	276	3:1	P = < .01	12.0 \pm 3.6
gl-3 - tw? ^{**}	276	excess for 15:1	P = < .01	1.0 \pm 1.7
Fl - tw?	276	"	P = < .01	
1 aleur. factor				
- tw3	579	"	P = .01	38.0 \pm 6.2
Fl - tw3	218	"	P = .02-.01	
gl - tw3	561	"	P = < .01	28.0 \pm 5.6

* This silky is one that appeared in an F₂ of a single cross here.

**This tw was linked in coupling with the gl-3, one of Stadler's mutants.

Negative results by the χ^2 for independence test were obtained for the following linkage tests: zb with lg; ws with Y Pl B rg; gl-1 with B lg nl?; nl? with B lg; ds-3 with su, pr Y colorless aleurone (9:7). gl6 with Y; gl9 with Y bt? and zg3 with Y and colorless aleurone (3:1)

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1. Gene Variability. The study of R alleles which Fogel and I reported in the 1943 News Letter has been continued, with the addition of a series of r^r types and with further study of specific modifiers of R action and of environmental conditions affecting it. All or nearly all of the 22 R's originally included appear to be distinguishable in their effect upon plant color, but since some of these differences are slight they require confirmation in experiments in which modifier action may be excluded more critically than is possible by repeated parallel backcrossing.

For this purpose we have used colorless aleurone mutants of several of the original R alleles, since as previously reported spontaneous mutations of R⁺ → r^r have no appreciable effect upon the plant-color action. For example six R alleles (Boone, 997, Cornell, Quapaw, Ponca, and Black Beauty) form a group characterized by rather strong pigmentation, though distinguishable in parallel backcrosses by slight though consistent differences. Colorless aleurone mutants of Cornell and Quapaw were crossed with other members of the group, and backcrossed by rg. This yields progenies in which the Cornell or Quapaw phenotype may be compared with the phenotypes of similar alleles in sib plants, the aleurone color difference providing a completely linked marker. Such comparisons, so far as they have gone, confirm the reality of the small differences observed between members of this group. A similar method may be used for the study of "non-linear" variation in the action of the different alleles (News Letter 1943, page 20), and here the mutant r^r's may be supplemented by naturally occurring r's. We are using the latter chiefly for this purpose.

The alleles of B (News Letter 1943, page 22) appear to be fully as variable as those of R, and since the range in plant-color phenotype is even wider, they may be better suited to the identification of small differences. Among 14 B^w's compared, 6 were selected as standards to represent distinct levels spaced roughly between b and B, and in each of these a stock of B-gl rg was established. These alleles listed in ascending order of effectiveness, are designated as follows:

- | | | |
|---------------------------------|-----------------------------------|-----------------------------------|
| 1. <u>B^w</u> (Boone) | 3. <u>B^w</u> (Clarage) | 5. <u>B^w</u> (Lookout) |
| 2. <u>B^w</u> (Young) | 4. <u>B^w</u> (La Paz) | 6. <u>B^w</u> (Seattle) |

Additional B^w's, both from existing stocks and from mutations of various B's, have been crossed each with the standard B^{w-gl} strains which appear to be just below and above them in effectiveness, and backcrosses of these hybrids will determine their position in the series. For further mutation work, Anderson's In2 (y4 B Gl lg) stock is being extracted in homozygous combination with rg since B^w mutations induced in this stock may be crossed with the naturally-occurring alleles to produce backcross progenies with virtually complete linkage of marker genes.

Miss Elizabeth Somers is making a detailed histological study of the development and distribution of anthocyanin under the action of R and of B.

2. Gene Action. Among tissues capable of anthocyanin production there are marked differences in response; cells of certain types produce

anthocyanin readily with any R-allele above the R3 level, while cells of other types may produce anthocyanin only in the presence of the strongest R alleles. For example, among epidermal cells of the leaf, there are distinctive differences in the reaction of the long, narrow cells over the veins, the long and short surface cells, the stomatal cells, the hairs and the specialized cells at the base of the hairs, and the paired siliceous and suberized cells. Anthocyanin is formed much more readily in the epidermis than in the underlying mesophyll cells, but in the chlorophyll-lacking sectors of japonica plants it is produced abundantly in mesophyll cells also. The same is true of certain white and virescent types, and in normal green plants the mesophyll cells of the auricle (which lack chlorophyll) are well colored by even relatively weak alleles. With strong B alleles, green mesophyll cells containing anthocyanin are more frequently found.

The alleles of R and B thus provide a series of reagents, so to speak, for the study of tissue differentiation. Thirty years ago Keeble, Atkins, and others showed certain interesting relations between anthocyanin patterns and the occurrence of oxidase systems detectable by the use of histochemical test-substances. Mr. Fogel has undertaken a study of this kind with maize, which is however still in a preliminary stage.

The study of competitive action of certain A alleles (News Letter 1943, page 21) is being continued in collaboration with John R. Laughnan. The dominant action of aP upon plant color is manifested with all of the visibly weakened A alleles tested (A^w, a^{lt}, A^{bc}, A^{rb}). The alleles A^{br} and A^{rb} (both obtained by Rhoades, out of a by Dt) are purple plant types distinguished from A by their reduced effect upon pericarp color. When these are compared with A in sib plants (in backcross progenies marked by et), they show slight but distinct reduction in anthocyanin pigmentation of the plant as well.

The dominant effect of aP upon plant color is shown also, to a slight extent, by certain A's which appear to have full plant color and pericarp color effect. The different A's used were extracted, after parallel backcrossing to a C R, from various stocks, chiefly the Indian strains used as foundation material for the R and B studies. With some A's the difference between A/aP and A/a sibs is clear enough to permit reasonably accurate prediction of the genotype at the flowering stage, and this identification may be made somewhat more accurately by testing the extracted pigment. The difference is due to the presence of varying quantities of yellow pigment in addition to the purple. With other A's and with A^b, no difference is found. The aP reaction thus serves as a sensitizer for the recognition of differences between the A alleles, and indicates the occurrence of considerable additional allelic variability at this locus. Conversely, the extent of the effect varies among different pale alleles obtained by mutation from A^b (News Letter, 1943, page 21), when these are tested against a common A. All of the pale alleles showing the dominant plant color effect have

dominant brown pericarp action; the two pale aleurone alleles with recessive brown pericarp (\underline{A}^w and \underline{A}^{lt}) give negative results in parallel tests.

Mr. Laughnan is making a chemical and spectrographic study of the pigments involved in the action of the \underline{A} alleles, and is developing methods for the quantitative study of the mixed pigment phenotypes.

3. Spontaneous Mutation. The frequency of spontaneous mutation to colorless aleurone types varies widely in different \underline{R} alleles. The most mutable of the alleles studied is \underline{R}^r (Cornell), which yields \underline{r} mutations at the rate of about 2 per 1000 gametes. At the other extreme are a few alleles which give no mutations in populations of 25,000 to 100,000 gametes.

As previously reported, differences in mutability are inherent in the gene itself, since they are maintained when a highly mutable and a rarely mutable allele are combined in a heterozygote, so that the mutations must occur in precisely comparable cells. This comparison is made possible by the fact that the mutations affecting aleurone color do not affect plant color, and in a heterozygote $\underline{R}^1 \underline{R}^2$, in which plant color is distinct in the two alleles combined, the identity of the gene mutating is readily determined. For example, when \underline{R} (Cornell) is combined with an \underline{R}^g of low mutability, the mutants produced by the F_1 plants are almost exclusively \underline{r} (Cornell).

In addition, however, there is a pronounced effect of modifiers upon the frequency of $\underline{R} \rightarrow \underline{r}$ mutation. Homozygous \underline{R} (Cornell) stocks extracted from crosses of the type mentioned show lowered mutation rates, in some cases much lowered. Different homozygous strains extracted from the same F_1 plant show distinctly different rates.

Mutations to colorless plant types ($\underline{R}^r \rightarrow \underline{R}^g$) occur at appreciable rates in certain alleles, and the variation between \underline{R}^r alleles in frequency of mutation to \underline{R}^g appears to be uncorrelated with that of mutation to \underline{r}^r . \underline{R} (Cornell) is very low in frequency of mutation to \underline{R}^g , while certain other \underline{R} alleles yield plant color mutations at moderately high rates, none however approaching the frequency of aleurone color mutations in \underline{R} (Cornell). The frequency of mutation to \underline{r}^r and to \underline{R}^g in the same plant (male germ cells) was tested extensively in 2 plants of \underline{R} (Columbia), with the following results:

Plant	Mutations to \underline{r}^r	Mutations to \underline{R}^g
1	6/12,525	3/11,804
2	<u>5/ 8,459</u>	<u>3/ 8,020</u>
Total	11/20,984	6/19,824

Mutations of \underline{R}^r to intermediate levels appear to be very rare. On the contrary \underline{B} mutates frequently to intermediate levels, and no mutations of \underline{B} to \underline{b} have been found. The \underline{B}^w alleles occurring by mutation differ widely in level of action. In this respect \underline{B} resembles \underline{A}^b , which as previously reported mutates frequently to different levels of \underline{a}^p type and rarely if ever mutates spontaneously to \underline{a} .

4. Comparison of X-ray and Ultra-violet Mutation. Following the experiment on X-ray and ultra-violet mutation of A previously reported (News Letter 1941, page 45-47, 1942, page 24-27), Roman and I set up a somewhat similar experiment with A^b. This was designed to take advantage of the fact that the spontaneous mutations of A^b are to an intermediate allele and are therefore clearly distinguishable from the effects of deficiency. The previous experiment had shown that the apparent mutations induced by X-rays were in fact minute deficiencies, and that the apparent mutations induced by ultra-violet were distinctly different and behaved as if they represented transformation of the gene to a recessive allele. It did not, however, exclude the possibility that the ultra-violet mutations were still more minute deficiencies, or cases of destruction of the single gene. With A^b this distinction could be made, if ultra-violet mutations actually are mutations of the type represented by spontaneous mutation of the same gene.

Extensive pollinations with untreated, UV-treated, and X-rayed pollen of a single A^b plant were made upon ears of a Dt, and numerous deficiencies and mutations were identified in the progeny. But the experiment failed in its main objective, because the natural frequency of mutation of A^b to aP is so high that no significant increase in aP mutations was produced by the treatments used.

The results, however, give additional support to the indication that the UV mutations are true gene mutations in two ways.

(1) No apparent mutation of A^b to a was found in the very extensive ultra-violet series.

(2) Among the endosperm mosaics induced by ultra-violet treatment, there were several cases in which a mosaic of clearly pale aleurone tissue showed typical dots of Dt type. Although an endosperm sector does not permit progeny testing, these can only have resulted from mutation of A^b to aP, induced by the ultra-violet treatment. An endosperm mosaic of pale appearance could result from any one of numerous causes, but it could not provide a background for visible dots of A tissue unless it resulted from a change in A-action, and this background could not be pale if the A loss were due to deficiency.

The effect of ultra-violet treatments upon A^b mutation is sufficiently frequent for detection in the endosperm and not in the embryo because of the much higher frequency of induced alterations in endosperm than in embryo, which has previously been reported as characteristic of ultra-violet treatment.

This heightened frequency of endosperm alterations may be used to simplify various studies involving ultra-violet effects, and to make possible certain studies which otherwise could not be carried out. For example, it would be very desirable to determine the effect of varying ultra-violet wave lengths on the frequency of mutation. The action spectrum for A-losses in endosperm has been determined, but these include both deficiencies and mutations, and presumably consist very largely of deficiencies. It would not be possible to make significant comparisons of wave length effectiveness in inducing mutation if the mutations could be identified only by the growing and testing of progeny plants.

The use of \underline{A}^b , with recognition of mutants by the \underline{a}^p phenotype, as described above, is effective for identifying positive cases of mutation in the endosperm, but it is not suited to quantitative work because of frequent failure of \underline{a}^p sectors to color positively. Laughnan and I have therefore made use of a different method, which permits identification of the alterations in the endosperm but with confirmatory tests on the plant grown from the accompanying embryo.

Pollen of homozygous $\underline{A} \underline{A}$ with the recessive markers $\underline{gl3}$ and \underline{j} was used on ears of $\underline{a-X1/a}^p$. The x-ray mutants $\underline{a-X1}$, $\underline{a-X2}$, etc., are inviable when homozygous and in all possible combinations inter se, and sectors homozygous or hemizygous for them are also inviable (News Letter, 1942, page 25). If all X-ray induced \underline{A} -losses involve the loss of the associated viability factor, X-rayed pollen will never yield a colorless seed or sector; if any apparently colorless or sectorially colorless seed is found, it may be tested by growing the plant to determine whether the female gamete was $\underline{a-X1}$ or \underline{a}^p . A colorless seed yielding a plant not heterozygous for \underline{a}^p is selfed or tested for the recessive markers to exclude the possibility of pollen contamination.

The \underline{A} -losses shown by \underline{a}^p tissue include the deficiencies plus the mutations among the seeds from \underline{a}^p gametes; those shown by \underline{a} tissue include the mutations alone among the seeds from $\underline{a-X1}$ gametes. Control pollination by $\underline{a} \underline{C} \underline{R}$ on a number of ears of the female stock show that \underline{a} gametes of \underline{a}^p and $\underline{a-X1}$ functioned in approximately equal numbers.

In the limited populations now completed, X-ray treatment has failed to yield colorless seeds or sectors. Ultra-violet treatment has given 3 proven cases of colorless sectors. The total number of \underline{A} -losses in endosperm in the ultra-violet population on which the tests have been completed was 92. This indicates a ratio of deficiency to mutation of about 86:3 under ultra-violet treatment for the \underline{A} stock used in the experiment. This is not greatly different from the proportion found among progeny plants representing \underline{A} losses in the embryo.

The induced alterations classified as mutations are subject to the same reservations regarding their genetic nature as are the ultra-violet mutations identified in progeny plants following treatment of \underline{A} . The method permits the determination of relative frequency of mutation (in this sense), with a fraction of the effort required in determining mutation from progeny plants. By this method it is feasible to compare the effect of different wave lengths upon deficiency and mutation simultaneously, and to compare different \underline{A} alleles in relative frequency of mutation. With slight modifications the method may be used also for the identification of gene mutations of \underline{A}^b critically distinguishable from the effects of gene-deficiency.

The results of the above experiment have a further interest in connection with the problem of the endosperm-embryo difference in frequency of ultra-violet alterations. The cause of this difference is unknown, and the most plausible guess has been that it is somehow connected with the difference in breakage-fusion phenomena in endosperm and embryo, which might appropriately be termed the McClintock effect. It might be expected that deficiencies, initiated by equal effects of the treatment upon the two sperm nuclei, might differ greatly in frequency of realization under

the very different conditions of endosperm and embryo. But this experiment indicates that the heightened frequency of alterations in the endosperm applies to mutations as well as deficiencies.

While the various experiments with induced mutation of A and A^b indicate that ultra-violet treatment produces true gene mutation and that X-ray treatment does not, they are disappointing in their failure to yield induced gene mutations which may be established in stocks subject to critical analysis. This is due to the failure of the A^b experiment described on an earlier page of this report. The advantage of regular spontaneous mutation to an intermediate allele, which makes A^b suitable for this experiment, applies also to R^r, since its spontaneous mutations are regularly to R^s rather than to r^s. In the case of R^r distinct alleles are available, including types with varying frequency of spontaneous mutation. Mrs. Elena Perak has undertaken an extensive study of the effects of X-ray and ultra-violet treatment upon mutation of various R^r alleles.

5. Effect of X-rays upon Dominant Mutation of a. No dominant mutations have been found in X-ray progenies of maize in experiments in which hundreds of recessive mutations have been observed. The evidence against the occurrence of dominant mutation induced by X-ray is however inconclusive, for the following reasons:

(1) The number of genes capable of showing dominant mutation may be much smaller than the number capable of showing recessive mutation, since many genes may be already fixed by natural selection at a level maximal for gene action. The possibility of inducing dominant mutation can, therefore, be tested critically only with known recessives.

(2) Among known recessives many may be themselves deficiencies and, therefore, incapable of dominant mutation. Critical evidence of failure to mutate to a dominant allele therefore may be obtained only from recessive genes which have previously been known to mutate to a dominant allele.

(3) The only recessive alleles which meet this requirement are the variegation genes, which may be regarded as unstable recessive mutating frequently to a dominant allele. In these the spontaneous frequency of dominant mutation is so high that an effect of X-rays in inducing additional dominant mutation probably would not be appreciable.

It is possible to avoid these difficulties in the case of one gene. The recessive dt has several known dominant alleles. The effect of Dt proves that it is capable of dominant mutation. In the absence of Dt it is not mutable, and would therefore permit recognition of even a slight effect of X-rays in inducing mutation. Since the effect of mutation is recognizable in minute sectors the treatment may be applied in a fairly advanced stage of endosperm development, so that many hundreds of cells are tested for mutation by the examination of a single endosperm. It is therefore possible to test for the occurrence of this mutation in practically unlimited populations.

The seed to be irradiated was produced by the cross a a X A a, both parents being homozygous for dt dt and for the complementary factors required for aleurone color. The endosperms of half of the seeds produced are A a a. These serve to indicate the size of sectors resulting from genetic

alterations induced by irradiation at the stage chosen, since induced deficiencies of A result in sectors of colorless aleurone. In the colorless seeds, induced dominant mutation of any one of the 3 a genes would result in a corresponding sector of colored aleurone. The colored seeds thus provide a basis for calculation of the number of opportunities for detectable mutation in the colorless seeds, and a basis for comparison of the relative frequency of induced dominant mutation and deficiency. Treatment was applied 73-81 hours after pollination.

The mutability of the a gene in both parental stocks was tested by crossing with adl Dt, adl being an a allele with negligibly low dominant mutation rate in the presence of Dt. From the results of these crosses the number of dominant mutations which would be expected in the a a a seeds under the influence of various doses of Dt may be calculated.

The results show failure of X-rays to induce dominant mutation in a population estimated at 5,700,000 cells, each containing three a's capable of mutation. The cell population of equal size in sib seeds yielded approximately 100,000 losses of A (deficiencies or recessive mutations) from cells containing only one A gene each. The number of mutations to A which would have occurred in the same populations under the influence of Dt, calculated from the test crosses mentioned, was over 16,000 for a single dose of Dt, or about 16 times this number for homozygous Dt Dt Dt seeds.

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During the past few years, a number of terminal deficiencies of the short arm of chromosome 9 have been isolated. Each deficiency arose as the consequence of a meiotic breakage of the short arm of chromosome 9 following crossing over in plants heterozygous for a chromosome 9 with a duplication of the short arm or for a structural rearrangement of the segments of chromosome 9. In each case, the extent of the deficiency was determined at pachytene in the F_1 plants which had received a normal chromosome 9 from one parent and a recently broken (deficient) chromosome from the other parent. Tests showed that deficiencies which ranged from minute to one-third of the distal segment of the short arm were all female transmissible. Those which extended into the first distinct chromomere were transmissible through the pollen. None of the longer terminal deficiencies were male transmissible. Because of the male and female transmission of the very short terminal deficiencies, plants which were heterozygous for these deficiencies were self-pollinated to determine if viable endosperms and embryos could be obtained which were homozygous for these deficiencies. In these F_1 plants, the normal chromosome carried c and the deficient chromosome carried C. The C mutant is located in the short arm within the 5th or 6th chromomere from the distal end. In these F_1 plants, 30 individuals were classified as having received a broken chromosome 9 which was deficient for only the knob. Self-pollinations of these heterozygous deficient plants gave typical ratios of 3 C to 1 c. The endosperms and embryos in both classes of kernels were normal. Plants arising from both the C and c kernels were likewise normal in appearance. Cytological

examination of some of these F₂ plants showed the presence of the two deficient chromosomes 9. It may be concluded that a homozygous deficiency of the knob does not obviously alter the appearance and functioning of any tissues.

Seven of the original F₁ plants were classified as having a chromosome 9 which was deficient for the knob and the adjacent segment of thin chromatin which joins the knob with the first distinct chromomere. Self-pollinations of these plants likewise gave typical ratios of 3 C to 1 c. The endosperms and embryos were normal in appearance. In all 7 cases, the seedlings arising from these kernels segregated in the ratio of 3 green to 1 pale-yellow. The pale-yellow seedlings are normal in morphology but die following exhaustion of food supplies in the kernels. Linkage of the pale-yellow phenotype with C, carried by the deficient chromosome, was obvious in each case. Through genetic and cytological means, it was possible to determine in each case that the recessive pale-yellow phenotype is produced as a consequence of the homozygous deficiency. Intercrosses between plants heterozygous for these 7 pale-yellow mutants showed that all 7 were either identical or allelic. The recessive mutant yg2 is known to be located close to the end of the short arm of chromosome 9. Combinations of a chromosome 9 carrying yg2 with any of the 7 deficient chromosomes 9 produced only normal green seedlings and plants. It may be concluded that the deficiencies which produce the pale-yellow phenotype are not long enough to include the Yg2 locus.

In six F₁ plants, the broken chromosome 9 was classified as being deficient for a terminal segment which extended into and included a part of the first distinct chromomere. These deficiencies were slightly longer than those which produced the pale-yellow phenotype. Following self-pollinations of these plants, normal F₂ ratios of 3 C to 1 c appeared in four of the six cases and a slight reduction of the C class in two of these cases. When these kernels were germinated, white seedlings segregated in ratios expected from a recessive mutant. In all cases, linkage of the white seedling mutants with C was obvious. It was possible to determine for each case that the white seedling phenotype resulted when these seedlings were homozygous for the deficient chromosomes 9. Intercrosses of heterozygous deficient plants of all 6 cultures were made to determine the allelic relations of the white seedling mutants. White seedlings segregated in the F₁ following all 15 combinations, indicating that the white seedling mutants were allelic if not identical. Intercrosses between plants heterozygous for the 7 pale-yellow producing deficiencies and the 6 white producing deficiencies gave rise to the typical pale-yellow phenotype in one-fourth of the progeny of all 42 crosses. It was determined that the pale-yellow phenotype arose following combinations of the two deficient chromosomes in a zygote. Thus, the deficiency mutants pale-yellow and white are allelic. Pale-yellow is dominant over white. This would be expected because the residual homozygous deficiency following combinations of the two deficient chromosomes is only that which would produce the pale-yellow phenotype.

Plants heterozygous for the 6 white seedling producing deficiencies were crossed by plants homozygous for yg2. In the progeny of all 6 crosses, a ratio of 1 green plant to 1 yellow-green plant appeared. Appropriate tests showed that the yellow-green plants were those which had received the

deficient chromosome 9 from the heterozygous parent. Therefore, it may be concluded that the white mutants are allelic to yg2, with yg2 dominant over white. This would be expected if the terminal deficiencies causing the white seedling mutants included the locus of Yg2. From the point-of-view of genetic analysis, the pale-yellow and white seedling mutants are comparable in all ways to other known recessive mutants in maize. The allelic expressions of pale-yellow and white and yg2 and white, and the non-allelic expression of pale-yellow and yg2 would be difficult to interpret following a purely genetic analysis. These results are readily interpretable when the cytological conditions are known. The phenotypic expression following combinations of any two of the three mutants may be considered a reflection of the residual effects of over-lapping deficiencies.

The mutants pale-yellow and white are repeatedly produced following the meiotic breakage of chromosome 9. Among 2577 such recently broken chromosomes 9 which were tested, 55 gave rise to the pale-yellow phenotype and 33 to the white phenotype. In contrast to most mutation inducing agents, the chromosomal breakage mechanism is a "mutation" inducing process which "induces" the same mutant time and again.

Barbara McClintock

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Unfortunately, I have been unable to make any worth while contribution to the News Letter. For the past few years my genetic research has been largely restricted to an attempt to keep some of my stocks from extinction in hope of better times to come.

I have, however, made fairly satisfactory progress with the sweet corn breeding. In a randomized block test that I ran last summer one of my hybrids out-yielded Golden Cross Bantam by about 85% (dry weight of shelled grain) and yielded about 90% as much as Trucker's Favorite. This Hybrid is perhaps 10-14 days earlier than T. F. and might average a little, perhaps a day, later than G.C.B. In quality, it is about the same as G.C.B. In what amount to "blind-fold" tests since the culture numbers meant nothing to the tasters, this hybrid got 15 votes and G.C.B. got 13 in direct comparison, a pretty good 1:1. Ears are slightly bigger but not quite so smooth as those of G.C.B.

In a smaller yield test planted about six weeks later, (hotter, drier weather and shorter days) this hybrid showed up much better in comparison with G.C.B.

Ioana and G.C.B. are the two sweet corns recommended for this area. Ioana was a little better than G.C.B. in the early tests but not nearly so good in the later test.

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1. Flint and Dent Corn. The improved yellow corn, Maiz Amarillo VENEZUELA -1, which is being distributed to the farmers of this country for commercial production, is neither dent nor flint corn but rather an intermediate between the two, with variations toward both extremes. This intermediate type, often referred to as tropical flint, is preferred to dent corn because it is more resistant to damage by the ever-present grain weevil.

Considerable difficulty has been encountered in maintaining this variety as a tropical flint. The farmers who make no selection in their corn complain that after two or three generations VENEZUELA-1 degenerates, that is, the amount of soft starch increases. Even in the Experiment Station where there has been selection for tropical flint ears during the past eight generations, the soft starch type reappears in considerable quantity at each harvest. The ears of the true flint type are scarce.

In this connection it is worthy to note that the dent corn from the United States and from Argentina become extremely soft under these conditions and little hard starch is developed.

2. Tall Corn. In the lowlands of this country where the soil is relatively fertile nearly all the local varieties of corn are extremely tall and the ears are often six to ten feet from the ground. The improved type, VENEZUELA-1, was especially popular when introduced to the public because it was shorter than the local varieties and had a low set ear. It has been discouraging to find that each year this corn is becoming taller and the ears are farther from the ground. Mass selection for low growing plants with their corresponding low set ears has been practiced for eight generations with little permanent success.

3. White Corn. Corn, prepared in a multitude of ways, is the principal food of the people of this country. Due to custom, the people of the central part prefer white corn while those of the eastern and western parts prefer yellow corn. When the corn improvement program was initiated in 1939, emphasis was placed on the selection of high yielding varieties of yellow corn with the hope that the people in the central region would take advantage of the improved seeds and perhaps learn to like yellow corn over a period of time, and thereby improve their diet. During the past two years this faint hope has been realized in certain areas in which the improved yellow corn, VENEZUELA-1, has given as much as 100% increase in yield over the local white varieties.

But in spite of this indication that a change in custom might be possible, we have finally yielded to public pressure to develop improved varieties of white corn (as a matter of fact, both white and yellow corn have been included in the corn improvement program since 1939, but the hybrids and the improved varieties of white corn have not been publicized). The few kernels of white corn which always appear in some of the ears of the variety Maiz Amarillo VENEZUELA-1 have been used as the basis of a new variety, Maiz Blanco VENEZUELA-3. From many thousands of ears of VENEZUELA-1, several hundred ears segregating white kernels were shelled together and planted in a small field. Before pollination the weakest plants

were eliminated. At the time of harvest, two kinds of ears were found: those with all of the kernels yellow and those with some kernels white and some yellow. The yellow ears were discarded. Of the ears with both white and yellow kernels, the best were shelled together and the seeds were placed on tables where a group of women picked out the white kernels by hand. (The white kernels were not all pure white; some were a faint yellow). They were planted in several experiment stations and with several farmers for propagation.

The harvest from these propagation plots was not completely white but is commercially acceptable. Further selection is being carried on to improve this new variety, VENEZUELA-3, but this slightly mixed type is being distributed to the farmers for commercial production. In the yield tests conducted in five different states this year, the varieties, VENEZUELA-3 and VENEZUELA-1, were nearly identical in plant type and in yield.

D. G. Langham

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V. SEED STOCKS PROPAGATED IN 1943

Dr. Murray and Miss Morris grew over 200 cultures and hand-pollinated approximately 1600 ears. These cultures consisted mostly of stocks that had been listed in earlier News Letters, that were in need of replenishing, or that were several years old and liable to loss of viability.

R. A. Emerson

MAIZE GENETICS COOPERATION

NEWS LETTER

19

February 15, 1945

The data presented here are not to be used in
publications without the consent of the authors.

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I. REPORTS FROM COÖPERATORS

Bureau of Plant Industry Station and Cornell University,
Beltsville, Md. and Ithaca, N. Y.

1. Tetraploid maize-Tripsacum hybrids. In 1942 the excised embryo technic was utilized to obtain two hybrids of tetraploid corn and tetraploid Tripsacum. Since these hybrids received two sets of chromosomes from each parent it was anticipated they would be fertile if the chromosomes comprising these sets synapsed to form bivalents. But these two hybrid plants proved to be completely sterile. They not only produced no functional pollen but when used as the seed parent in backcrosses to their parents no viable seed was obtained from them. A variable number of bivalents were formed and in addition there were always present from one to several multivalent complexes that could not be fully analyzed.

Compared with the elaborate technic of Mangelsdorf and Reeves a relatively simple procedure was employed to obtain these hybrids. The husks of the earshoots were opened sufficiently to permit a mixture of Tripsacum and corn pollen to be sifted in about the bases of the silks, the husks were then replaced about the earshoot and held in position by the glassine earshoot bag reinforced with rubber bands. Approximately three weeks after pollination the embryos of the partly developed kernels were excised and cultured in two ounce screw cap bottles on the sterile nutrient medium employed by Randolph and Cox for the culture of iris embryos (Proc. Amer. Soc. Hort. Sci. Vol. 43, 1943). As soon as a root system and seedling leaves were formed the seedlings were transferred to soil.

The two hybrids produced in 1942 resulted from the pollination of 14 earshoots of a synthetic tetraploid corn hybrid involving 5 different yellow dent lines (Stock A in accompanying table) with a mixture of tetraploid Tripsacum and tetraploid corn pollen carrying a full complement of genes for colored aleurone. Corn pollen was included with the Tripsacum pollen because Mangelsdorf and Reeves found that the presence of a certain number of normally developing corn grains on the ears aided the development of any rare hybrid kernels that might result from the functioning of Tripsacum pollen. Colored aleurone was involved to facilitate the separation of hybrid from the non-hybrid seeds.

In 1943 a further attempt was made to obtain additional hybrids for a more adequate study of their characteristics. Four vigorous tetraploid hybrids of commercial lines of yellow dent corn were selected as the seed parents. From a total of 88 pollinations 68 immature embryos or embryo-like structures were cultured. Most of these were inviable and the eight seedlings obtained from them proved to be non-hybrid corn seedlings.

The stocks used in 1944 to repeat the cross differed from those used in the preceding two years. These are listed as stocks B-F in the following table which summarizes the results obtained in 1942 and 1944. Stock B was a multiple recessive tetraploid combination of one or more recessive genes in each of the ten chromosomes (P^V -bm2, b-lg, A-cr, su, pr, y-pl, in, j, c-wx, R^E -g). Stocks C, D and E were, with respect to most of these recessives, duplex heterozygotes, the recessive stock having been crossed with an aB Pl lg type to produce C, and AB Pl R^E type to produce D and with the inbred 187-2 to produce E. Stock F was an F_1 hybrid of two commercial yellow dent lines, one of which was 187-2.

Stock	Ears pol.	Embryos cultured	viable hybrid seedlgs.	Non-hybrid corn seedlgs.
A	14	78	2	26
B	22	0	0	0
C	6	13	5	9
D	8	14	4	3
E	7	4	1	2
F	10	2	1	0

Perhaps the most interesting conclusion to be drawn from the results of these attempts in 3 different years to obtain hybrids between tetraploid corn and tetraploid *Tripsacum* is that hybrids may be obtained much more readily from certain stocks than from others. Gene differences affecting crossability may be involved, or, if the suggestion of Mangelsdorf and Reeves that corn carries segments of *Tripsacum* chromatin is to be taken seriously the possibility that such segments were present in the stocks which crossed most readily should be considered. However, there were no pronounced differences in knob frequency in the Stocks A-F; all had relatively few knobs.

The hybrids obtained in 1944 have not yet reached the sporocyte stage. One of the hybrids obtained in 1942 produced abundant tillers and has been maintained by vegetative propagation without difficulty; the other 1942 hybrid was less vigorous, produced few tillers and could not be kept alive by vegetative propagation. Extreme differences in the vigor of the 11 hybrids obtained from the 1944 crosses suggest that they may differ appreciably with respect to their chromosomal configurations.

2. Trisomic stocks. The number 1 trisome has been identified cytologically in stocks which gave trisomic ratios for bm₂. All of the 10 trisomes have now been isolated and stocks of these are available in cultures known to be free of supernumerary B-type chromosomes.

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Inheritance of susceptibility to Helminthosporium carbonum Race I. There are here submitted preliminary data on the linkage relations of the gene hm governing susceptibility to infection by H. carbonum Race I.

Earlier studies (Jour. Agri. Res. 63:331-334, 1941) and (Phytopathology 34: 214-222, 1944) have shown susceptibility to infection by H. carbonum Race I to be inherited as a monogenic recessive. Appropriate crosses were made by Dr. E. G. Anderson using a series of translocation stocks in which su endosperm was used as a translocation marker. The parents Pr and K61 are homozygous susceptible inbred lines of normal dent corn. The F₁ material was backcrossed with pollen from double recessives (sugary susceptible plants). Kernel separations were made of the backcross progenies, planted in the greenhouse and seedling inoculated at the 3-4 leaf stage. One week after inoculation disease readings were made. The data in table 1 definitely indicate that the gene hm is located on chromosome 1.

In table 2 a summary is given of a four-point test involving 9 backcross progenies. Further studies are underway in which backcross progenies $\frac{p \text{ hm } br}{+ + +} \times \frac{p \text{ hm } br}{p \text{ hm } br}$ will be used. A series of translocations all involving chromosome 1, and supplied by Dr. E. G. Anderson, will also be under observation in 1945.

Table 1. Segregation of seedlings in which su endosperm was used as a marker for translocations

F ₁	Number kernels planted*				Chi Square		Range of "P"
	Sug.	St.	Res.	Sus.	Res.	Sus.	
suT1-4a x Pr	1344	1149	921	317	190	912	767.0 < .01
K61 x suT1-4a	924	894	664	176	150	703	642.0 < .01
suT2-4a x Pr	408	475	173	207	234	341	3.1 .2 - .3
K61 x suT2-4a	541	675	223	259	319	344	3.6 .1 - .2
suT2-4c x Pr	566	512	266	239	245	238	1.5 .3 - .5
K61 x suT2-4c	516	511	240	237	248	237	.3 .5 - .9
suTuT4-5b x Pr	458	476	199	206	230	230	.1 .5 - .9
K61 x suTuT4-5b	250	273	120	114	133	139	.3 .5 - .9
Pr x suT4-6a	478	495	190	205	240	221	1.3 .5 - .9
K61 x suT4-6a	443	484	187	181	255	218	3.0 .2 - .3
Pr x suT4-8	336	437	157	161	224	188	.2 .5 - .9
Pr x suT4-9a	548	545	227	219	244	249	.8 .5 - .9
K61 x suT4-9a	252	251	114	109	115	128	3.2 .2 - .3
K61 x suT4-10b	257	245	127	125	112	119	.2 .5 - .9

* Also represents kernel ratio found on ears

Table 2. Four-point test for the gene hm, the F₁ genotype being hm + + +
+ br f bm₂

Parental		Com-		Reg.		Reg.		Reg.		Reg.		Reg.		Reg.		Total
Progeny No.	binations	1	2	3	1 & 2	1 & 3	2 & 3									
1	1	31	3	11	0	2	19	43	3	4	3	3	2	3		158
2	61	50	11	20	2	6	47	53	9	1	7	9	0	16		292
3	45	54	8	19	2	10	40	45	7	0	8	13	0	8		259
4	46	53	11	12	2	8	33	36	4	6	10	12	2	9		244
5	58	53	8	6	1	7	46	51	4	0	3	6	1	3		247
6	47	52	12	19	3	6	55	45	6	1	12	6	5	9		278
7	53	62	13	13	1	8	29	54	3	0	7	7	2	6		258
8	73	37	4	22	0	6	29	44	7	0	7	9	0	21		259
9	45	46	5	12	3	7	29	64	6	3	3	8	1	3		235
	459	438	75	134	14	60	327	435	49	15	60	73	13	78		
Total		897		209		74		762		64		133		91		2230
				9.4%		3.3%		34.2%		2.9%		6.0%		4.1%		

The indicated genetic map is:

hm 18.3 br. 10.3 f 44.3 bm₂

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The following tables are compiled for the benefit of those using or wanting to use the sugary and waxy series of translocations for the study of economic or other characters in maize. The data included in tables 1 and 2 are the per cent of crossing over with su or wx in the heterozygous translocation plants, the position of the break in the other chromosome, and which alleles of Su su or Wx wx are present in each translocation. Tables 3 and 4 give a list of new semisteriles which small test plantings have shown to be linked to su or wx.

Table 1. Translocations closely linked with sugary.

	Crossing over with su	Chro- mosome	Cyto- logical position	Linkage	Gene Combinations available
1-4a	3.0	1		br-20-T-45-bm ₂	Su su
2-4(K-10)	(2.)	2		near B (± 8)	Su su
2-4(C-31)	close	2		near B (± 17)	Su
✓ 2-4a	3.5	2	2L.2	B-T-1.5-Y ₄	Su su ✓
2-4C	9.2	2		Y₄ -19.0-T-29.2-Ch	Su su
2-4(A-29)	6.1	2		Y₄ -22.3-T	Su su
✗ 4-5C	1.1	5		bm-3.5-T-15.5-pr	Su
✓ 4-5d	1.9	5		bm-2.5-T-5.5-pr	Su su ✓
4-5(X-6-77)	9.0	5		pr ± 16.4	Su su
4-6a	4.5	6	6L.3	very close to Y	Su su
4-6C	2.	6		very close to Y	Su
4-7a	close	7	7L.3	near ra and gl	Su
4-8a	close	8	8L.1	T-34-msg-j	Su su
4-9(F-22)	4.2	9		c-wx-6.9-T	Su su
4-9a	{ 3. 20	9	9L.8	{ c-wx-11.5-T c-wx-31.0-T	Su su
4-9(A-26)	close	9		not tested	Su
4-10 b	4.0	10		near g	Su su
4-10(B-45)	close	10		T-8.8-g-R	Su
1,3,4,5,(B-2)	close	1,3,5		1 not tested, 3 near ts ₄ , 5 near bm	Su su

Table 2. Translocations closely linked with waxy.

	Crossing over with <u>wx</u>	Chro- mo- some	Cyto- logical position	<u>Linkage</u>	<u>Gene combinations</u>
1-9C	12.1	1	1S 6	P-0.8-T	Wx wx
1-9a	11.2	1	1S.	P-21.2-T-35.6-br	Wx wx
2-9b	7.5	2	2S.1	ts ₁ -5.3-T-7.8-√4	Wx wx
3-9a	3.6	3		near ts ₄	Wx wx
3-9C	7.6	3	3L.1	near ts ₄	Wx wx
3-9b	6.8	3		lg2-7.9-T-18.0-a ₁	Wx wx
4-9 (F-22)	6.9	4		su-4.2-T-Tu	Wx wx
4-9b	3.1	4	4L.6	su-Tu-13-21.9-T	Wx wx
5-9a	2.0	5	5L.6	bm ₁ -pr-25-T	Wx wx
5-9 (X-14-111)	near wx	5		(near pr)	wx
6-9a	9.4	6	6S.	T-12.9-Y-P1	Wx wx
6-9b	3.8	6		near Y	Wx wx
6-9 (a-66)	12.2	6		near Y	Wx wx
6-9 (X-25-78)	3.4	6		near Y	Wx wx
8-9a	13.7	8	8L.2	T-30-msg-j	Wx wx
9-10b	5.7	10		T-8.8-g-R	Wx wx
9-10a	4.5	10	10L.9	g-R-3.2-T	Wx wx

Table 3. New semisteriles linked with sugary.

	Backcrosses with su <u>Total</u>	<u>Crossovers</u>	<u>Gene Combinations</u>
a-57	36	0	Su
I-10	38	3	su
K-17	107	3	Su su
X-1-1	39	3	Su su
X-2-64	36	2	Su su
X-17-108	near su		su
X-19-5	near su		su
X-47-41	39	0	su
X-57-31	30	1	su

Table 4. New semisteriles linked with waxy.

	Backcrosses with wx		Gene
	<u>Total</u>	<u>Crossovers</u>	<u>Combinations</u>
a-76	34	2	Wx
F-24	96	7	Wx wx
bp	near wx		wx
X-7-39	40	3	Wx wx
X-10-6	37	0	wx
X-11-73	37	5	Wx wx
X-22-92	39	1	Wx wx
X-23-158	39	5	Wx wx
X-26-8	35	2	Wx wx

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Translocations and centromere positions. Translocations are especially useful in determining the location of genes in relation to the centromere and other visibly differentiated regions of the chromosome, due to the fact that their position in the chromosome can be determined cytologically and their linkage relations with known genes also can be determined. The following is a summary of available data on the relative positions of translocations and genes in the neighborhood of the centromeres in chromosomes 1 to 9 inclusive, with a few records for chromosome 10. These data were compiled chiefly from Dr. Anderson's records while in residence at the California Institute of Technology for several months in 1942 and 1944.

Chromosome 1. - Information on translocations in the short arm of chromosome 1 was summarized by Anderson in 1941. The gene P is about two-thirds of the distance out on the short arm. A minimum map distance from P to the centromere may be determined from % 1-9a which is known to be located in the short arm. On the basis of 730 plants the per cent of crossing-over between P and T 1-9a was found to be 21.2 ± 2.5 . Thus the location of the centromere in the linkage map is 21.2 units or more to the right of P.

A number of translocations in the long arm of chromosome 1 give less than 5 per cent of the crossing-over with brachytic. These are distributed from about L2 to about L6. The gene br is probably located in the neighborhood of L3 or L4. Only 2 of the translocations in the long arm are definitely placed to the left of br. T 1-6a was reported by Burnham and Cooper and Cooper and Burnham to be in the

long arm of chromosome 1 a short distance from the spindle insertion. From their diagrams and figures a position of about L2 is indicated, which is also in accord with other data. The map position, based on 75 plants, is given as 13.4 units to the left of br. T 1-6b has been described by Burnham. The locus in chromosome 1 is given as L2.5. Very good linkage data involving 952 plants place the translocation to the left of br with 3.8 per cent of crossing over. (Data by Burnham cited by Emerson, Fraser and Beadle, 1935). These data merely show that br is between one-quarter and one-half the distance out on the long arm. The map position of the centromere must be some where between the locus of T 1-9a, 21.2 units to the right of P and the locus of T 1-6a, 13 units to the left of br. This is a very long region. If crossing over were equally distributed over this portion of the chromosome we might expect the centromere to be about midway between P and br.

Chromosome 2. - The map location of the centromere can be rather closely delimited by a number of translocations in the interval between ts and v₄. Several of these will be considered. T 2-9b is located cytologically at 2S1 and 9L2. Linkage tests give the order definitely as B-ts-T-v₄. Crossing over between the nearest genes was

$$\begin{aligned} \text{ts-T} &= 33/622 = 5.0 \text{ per cent} \\ \text{t-v}_4 &= 121/1528 = 7.9 \text{ per cent} \end{aligned}$$

Since the break in chromosome 9 is known to be in the long arm (Anderson, 1938), the wx gene is carried in the 9² chromosome. Tests of linkage relations in the homozygous translocation can be used to verify the location of the break in chromosome 2. These tests gave the following results, showing that the break is between ts and v₄.

$$\begin{aligned} \text{B} - \text{ts} &= 27\% \\ \text{ts} - \text{v}_4 &= 55\%, \text{ or independence.} \\ \text{wx} - \text{B} &= 21.3\% \\ \text{wx} - \text{v}_4, \text{ repulsion series} &= 51.5\% \\ \text{wx} - \text{v}_4 \text{ coupling series} &\text{ in } 50.1\% \end{aligned}$$

The wx gene is carried in the 9² chromosome.

The linkage of wx with B and its independence of v₄ establishes the break in the short arm of chromosome 2 between B and centromere. The linkage of B and ts shows the break in to the right of ts and the independence of ts and v₄ locates the break between those genes. Thus the centromere is at least 5 units to the right of v₄.

T 2-5a was studied by Rhoades and described cytologically as in the long arm of chromosome 2 near the centromere. Linkage tests give the order as B-T-v₄ with 7.3 per cent of crossing over between T and v₄.

T 2-10a is located at L2, with the break in chromosome 10 well out on the long arm, 2 to 3 cross-over units to the left of g. The order on chromosome 2 is ts-T-v₄ and the data on crossing over are as follows:

$$\begin{aligned}\underline{ts}-T &= 11.4 \text{ per cent} \\ T-\underline{v}_4 &= 6.6 \text{ per cent}\end{aligned}$$

Linkage data in the homozygous translocations are as follows:

$$\begin{aligned}\underline{B}-\underline{ts} &= 16.+ \text{ per cent} \\ \underline{B}-\underline{g} &= 20 \text{ per cent}\end{aligned}$$

Since g is distal to the break in chromosome 10 the B-ts section of chromosome 2 must include the centromere, i.e., the translocation must be in the long arm of chromosome 2.

These data may be summarized as follows:

$$\begin{array}{lll}T\ 2-9b & \underline{ts}-5.0-T-7.9+-\underline{v}_4 & \text{short arm} \\ T\ 2-5a & \underline{ts} \quad -T-7.3 -\underline{v}_4 & \text{long arm} \\ T\ 2-10a & \underline{ts}-11.4-T-6.6-\underline{v}_4 & \text{long arm}\end{array}$$

The centromere must be 5 or more cross-over units to the right of ts and 7.3 or more units to the left of v₄. Since there is usually some suppression of crossing over in the heterozygous translocations, the total map distance of the ts-v₄ interval is uncertain. The normal value is probably about 20 units. The centromere is probably a little closer to ts than to v₄.

Chromosome 3. - The summary of translocations involving chromosome 3 published by Anderson and Brink places the centromere in the general neighborhood of ts₄. Since then additional data on T 2-3b has indicated that ts₄ is in the long arm of chromosome 3. This translocation shows about 4 per cent of crossing over with v₄. The order is probably B-sk-v₄-T. Linkage tests in homozygous T 2-3b stocks give the following cross-over values.

$$\begin{aligned}\underline{B}-\underline{sk} &= 39/399 = 9.+\% \\ \underline{B}-\underline{v}_4 &= 128/289 = 44.3\% \\ \underline{B}-\underline{ts}_4 &= 495/1171 = 42.3\% \\ \underline{ts}_4-\underline{lg}_2 &= 27/135 = 20.0\% \\ \underline{v}_4-\underline{ts}_4 &= 10/59 = 17.+\%\end{aligned}$$

These data all agree in placing the translocation beyond v₄, consequently in the long arm of chromosome 2. The linkage of ts₄ with B and v₄ in the homozygous translocation places the break between the centromere and ts₄, and shows that it is the long arm that is involved. From this it may be concluded that the centromere is to the left of ts₄, i.e., between d and ts₄.

Chromosome 4. - A number of translocations in the proximal regions of both arms of chromosome 4 adjacent to the centromere all show close linkage with su, usually accompanied by much suppression of crossing over. These data indicate that the centromere is in the general region of the su locus. Data on T 2-4c place su in the short arm. This translocation is very near the centromere in the short arm of chromosome 4, and is far out on the long arm of chromosome 2 between v₄ and ch. Linkage data from homozygous T 2-4c show ts₅ and su to be linked and su to be independent of Tu. Thus the break is to the right of su. Further data on this homozygous translocation areas follows:

$$\begin{aligned}\text{su-v}_4 &= 401/1057 = 37.94 \text{ per cent} \\ \text{su-ch} &= 247/525 = 47.0 \text{ per cent} \\ \text{Tu-ch} &= 193/429 = 44.9 \text{ per cent}\end{aligned}$$

From heterozygous stocks of this translocation chromosome 2 linkage relationships and adjacent to the break were:

$$\begin{aligned}\text{v}_4-19.94\text{-T-}29.3\text{-ch} \\ \text{for chromosome 4:} \\ \text{su-9.1-T-}30.8\text{-Tu}\end{aligned}$$

The linkage of su with v₄ in the homozygous translocation demonstrates that the translocation must be between su and the centromere of chromosome 4. This places the centromere at least 9 units to the right of su on the linkage map.

Chromosome 5. - The position of the centromere in relation to the known genes of chromosome 5 was determined very accurately by Rhoades in 1936, with the aid of a fragment of chromosome 5, which apparently consisted of the centromere and the entire short arm of the chromosome. In the metaphase of the first meiotic division in the microsporocytes the fragment formed a trivalent with the two normal number 5 chromosomes in approximately half of the cells; in the remainder of the cells it was present as an univalent that was rarely included in either daughter nucleus. From the known cytological behavior of the fragment the expected back cross ratio from fragment plants of the constitution AAa with a in one of the normal chromosomes was calculated to be 5A:3a or 37.5 per cent of recessives. This ratio differs sufficiently from the ordinary 1:1 back cross ratio of disomic inheritance so that with the aid of the fragment chromosome genes located in the short arm could be distinguished from those located in the long arm of chromosome 5.

Another test employed by Rhoades to identify the genes in the short arm was the occurrence of fragment-carrying plants homozygous for the recessive gene in the back cross progenies of fragment plants carrying a recessive allele in one of the normal number 5 chromosomes. If the locus under consideration was in the short arm none of the

fragment-carrying plants would be homozygous for the recessive allele, barring rare exceptions resulting from chromatic crossing over.

Utilizing these tests it was found that the A₂ and bm loci were in the short arm and bt, pr, ys, v₂ and v₁₂ were in the long arm of chromosome 5. The available cytological and genetical data from translocations involving chromosome 5 confirm the findings of Rhoades relative to the position of the centromere between the bm and bt loci.

Chromosome 6. - There are available six translocations recorded cytologically at about 6L2 or 6L2.5. These are T 1-6c, 2-6c, 4-6a, 4-6b, 4-6c and 6-9b. All are closely linked with Y and are definitely to the left of Pl. All show a reduction of crossing over between Y and Pl to 5% or less, in the heterozygous condition. Proven cross-overs with Y have not as yet been obtained for study. With so much suppression of crossing over, little can be inferred as to the location of the Y locus with reference to the centromere. Translocations in the satellite or nucleolar region are located well to the left of Y. Data on 3 translocations between the centromere and the nucleolar region are too meagre to give any satisfactory evidence as to the position of the centromere.

Chromosome 7. - Translocation 2-7b is located about one-fourth of the way out on the long arm of chromosome 7 and at about the same relative position on the long arm of chromosome 2. Linkage tests place it near ra, with slightly less than one per cent of crossing over. Linkage tests in the homozygous translocation show linkage of ra and gl, which places the translocation to the left of ra. This is also confirmed by the linkage of B and ra ($B-ra=167/462=36.1\%$). Since B is in the short arm of chromosome 2 and is thus in the 2nd chromosome ra must be in the translocated portion of chromosome 7. Several translocations in the short arm of chromosome 7 have been tested for linkage with ra as follows:

T 1-7d	S ₄	5/231	=	2.2%
T 2-7c	S ₁ +	24/376	=	6.4%
T 5-7d	S ₁	14/153	=	9.2%

Chromosome 8. - The only gene known to be located in chromosome 8 are in the distal region of the long arm. From the data of Anderson (1939) the location of the centromere must be 30 units or more to the left of msg.

Chromosome 9. - Translocation 5-9a is located in the short arm of chromosome 9 near the centromere and is about 2 cross-over units to the right of wx. This places the centromere at least two units to the right of wx. T 3-9a in the long arm of the chromosome gave 3.6% of crossing over with wx, indicating that the centromere is probably not far beyond the minimum of 2 units. The gene y has not

been located definitely but is believed to be in the long arm not far from the centromere (Beadle 1932, Burnham 1934b). Its map position is 12 units from wx.

Chromosome 10. - The only chromosome 10 genes which have been tested with translocations are g and R. Both are located far out on the long arm, apparently beyond L.6. Translocations to the left of L.3 have given from 9 to 23 per cent of crossing over with g. Probably there are different amounts of suppression involved. The centromere must lie at least 15 units to the left of g.

8-10a	S.6	17.0	104/613
8-10c	S.4	22.8	122/535
9-10b	L.1-	8.8	12/135
6-10a	L.1	9.6	33/342
3-10a	L.1+	15.7	74/471
1-10a	L.3	15.3	21/137

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1. Linkage relations of the bronze locus. F_2 data suggested that bronze (b_z) belonged in chromosome 9 and was located to the left of C. Backcross data obtained this past year show that the order is C-sh-b_z with b_z approximately 2 cross-over units from sh.

Summary of $\frac{C \ Sh \ bz}{c \ sh \ Bz} \times c \ sh \ bz$

(0)	(0)	(1)	(1)	(2)	(2)	(1-2)	(1-2)
C	c	C	c	C	c	C	c
Sh	sh	sh	Sh	Sh	sh	sh	Sh
<u>bz</u>	<u>Bz</u>	<u>Bz</u>	<u>bz</u>	<u>Bz</u>	<u>bz</u>	<u>bz</u>	<u>Bz</u>
1396	1354	76	65	15	31	0	0

C-Sh 4.8% recombination
 Sh-Bz 1.6% "
 C-Bz 6.4% "

Summary of $\frac{Sh}{sh} \frac{Bz}{bz}$ x $sh\ bz$

Sh	Sh	sh	sh	Total	6040
Bz	bz	Bz	bz		
<hr/> 2952	<hr/> 54	<hr/> 62	<hr/> 2972		

Sh-Bz 1.92% recombination

2. Cross sterility. A new mutant was found in 1942 showing a chlorophyll striping. No seeds were obtained from a large number of crosses in which this mutant plant was used as the female parent although these plants were self-compatible. Normal siblings were self- and cross-compatible. In many ways this situation is comparable to that previously reported by Demerec for crosses involving rice pop as the female parent.

3. Blotched aleurone. In the 1935 linkage summary the blotched aleurone gene (Bh) was shown to give 26% recombination with Y; no other linkages involving Bh were reported. This past summer I obtained data showing that Bh was close to Pl. I mentioned this to Dr. Emerson and he dug up from his old records data which show the same close linkage. I was interested in the Bh locus because of the Bh-c interaction. As Emerson found out years ago seeds of A R c Bh are not colorless but have irregular patches or blotches of color in the aleurone. In order to test the hypothesis that Bh was a gene stimulating the mutability of recessive c in the same way that Dt affects a I made a number of crosses involving a chromosome 9 lacking the C locus. The deficient chromosome 9, obtained from McClintock, had lost that portion of the short arm from the terminal knob to and including the C locus. Sh was not included in the deficiency. Plants carrying this deficient chromosome with the Sh allele and a normal chromosome 9 with recessive c and sh were pollinated by c sh Bh pollen. The Sh seeds had the C locus represented by a single recessive c allele while the sh seeds had three recessive c alleles. The two classes of seeds were examined for the grade of blotching. The data clearly show that seeds with one c allele have less aleurone color than do seeds with three c alleles. The Sh and sh phenotypes have no effect on the degree of blotching. This dosage effect of c would seem to indicate that the Bh-c situation is comparable to the Dt-a.

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1. Six deviating lines, originating as mutations in long inbred strains, have been compared in the heterozygous condition with their normal and deviating homozygous parental lines. In all cases there was an increase in size of plant (height, width of leaf, width of stalk) and in yield of grain and a hastening of the time of flowering when compared to the mean of the parents. When compared to the larger or earlier parent in each case there are definite increases in yield in four cases ranging from 17 to 104 per cent. Increases in height in four cases varied from 3 to 9 per cent over the taller parent. Time of flowering was intermediate in two cases and earlier than the earlier parent in two cases.

When outcrossed to unrelated normal lines and compared to the same crosses made with the normal parent the differences are small and show significant increases for the deviating line in only one case. Due to the very dry season and poor location this trial is not as conclusive as it may be possible to obtain.

In every case except one the deviating line is less productive than the line from which it originated and thus appears to be a degenerative change. A narrow leaf variation produces taller plants which flower earlier than the normal line. The stalk is more slender and has much less leaf area. This deviating line in previous years has been noticeably less productive but in the replicated yield test this last year it proved to be considerably more productive. Possibly this is due to the earlier maturity in a very dry year. If it proves to be more productive from now on it will be the first variation in inbred corn to be better in ability to reproduce its kind.

2. Attempts to shorten corn plants for convenience in pollination were not entirely successful. Two single crosses (Hy x L317 and Hy x 540) planted at two different times, May 27 and June 8, were bent to the ground and tied with binder twine to the adjoining plant on July 14. At this time the first planting was 3-4 feet and the second planting about 2 feet high. The plants were about one foot apart in the row. All of the plants had such a strong pull toward the erect position that all were injured to a certain extent by the string cutting into the stalks. Some plants were completely severed below the growing point and thus committed suicide rather than be tied down! Short plants were tied above the growing point. These bowed upwards between the base and place of attachment and tried to grow out of the leaf sheaths and were badly stunted. The treated plants in both plantings were shortened about 15 inches in ear height. The first planting was shortened 22 inches in average height of stalk to tip of tassel and the second planting 11 inches. The treated plants were also delayed a day or two in time of tasseling and silking. Both

pollen and seed production were seriously reduced by this treatment. Possibly the plants can be tied more loosely using a larger and softer cord. Care must be taken to tie the plants well below the growing point.

Plants that were bent over and covered with soil straightened out and were not reduced in height or delayed in flowering. Plants with half of each leaf cut off before flowering were not shortened in height but were so delayed in flowering that many of them never produced either tassels or ears!

Plants grown from seeds in which the embryo was cut out and attached to endosperms of the same or different genetic constitution were kept in the greenhouse for several weeks and later set in the field. Compared with untreated plants of the same type these plants were noticeably shortened. Since other plants grown for an equal length of time in the greenhouse were not shortened it may be that the embryo excision had something to do with this change.

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1. White-capped red pericarp. In News Letters 16 and 17 (1942 and 1943), I presented data indicating that white-cap red pericarp of such varieties of maize as Bloody Butcher is not a member of the multiple allelic series at locus P as has been supposed and suggested that this color is conditioned by multiple genes as in quantitative inheritance, one or more of which are closely linked with P. In Bloody Butcher white-cap red pericarp is associated with red cob (C-R), while in Northwestern Dent an apparently identical pericarp color is associated with white cob (C-W). Northwestern Dent alone was involved in the earlier work which had lead to the idea that white-cap red was allelic to P, and Bloody Butcher alone was involved in the results reported in recent News Letters. It became important, therefore, to repeat the study with Northwestern Dent in order to determine whether the apparently identical pericarp color of the two varieties is inherited in the same way. Results to date indicate that intensity of color of white-cap red of Northwestern Dent also is conditioned by multiple genes, one or more of which are linked with P. But certain complications have arisen which give the whole problem added interest---not to say added perplexity.

For comparison with more recent data, there are here presented records from News Letter 16 (1942), including F_2 and backcrosses of Bloody Butcher, C-R, with colorless inbreds, W-W. Pericarp-color grade "0" is colorless and "6" is about the intensity of Bloody Butcher.

Table 1.

	Cob Color	Pericarp-color grades 0 - 1 - 2 - 3 - 4 - 5 - 6							Total	Mean grade
C-R/W-W	{ R	32	4	45	58	72	113	17	341	3.6
	{ W	49	4	24	25	13	3	--	118	1.6
$\frac{C-R}{W-W}$ /W-W	{ R	48	6	38	41	40	37	2	212	2.7
	{ W	119	2	7	41	28	5	--	202	1.4

Cob color here shows approximately normal mono-genic segregation, but the ratios of colored to colorless are not those typical of mono-hybrids. The mean grade of pericarp color of red-cob segregates is materially higher than that of white-cob ones. The four possible combinations of cob color and pericarp color appear with frequencies indicating linkage.

The same type of cross was repeated with F_4 C-R and W-W segregates from the original Bloody Butcher cross. The results are:

Table 2.

	Cob	0 - 1 - 2 - 3 - 4 - 5 - 6							Total	Mean
C-R/W-W	{ R	--	5	5	17	34	39	3	103	4.0
	{ W	5	5	7	11	2	--	--	30	2.0
$\frac{C-R}{W-W}$ /W-W	{ R	--	1	4	30	29	9	--	73	3.6
	{ W	31	5	14	15	--	--	--	65	1.2

Here again segregation of cob color is normal and the mean pericarp-color grade is higher for red-cob than for white-cob segregates. But one color-class, W-R, did not occur and the ratios of colored to colorless pericarp are far from those typical of mono-hybrids.

White-cap red pericarp of Northwestern Dent, associated with white cob, C-W, also has now been studied. Crosses of this variety with a red-cob colorless-pericarp inbred, W-R, selfed and crossed with W-W are recorded below.

Table 3.

	Cob	0	1	2	3	4	5	6	Total	Mean
C-W/W-R	{R	31	21	19	33	24	12	2	142	2.3
	{W	--	2	3	9	11	13	7	45	4.0
C-W/W-R W-R	{R	83	--	1	--	--	--	--	84	.02
	{W	1	16	19	18	5	--	--	59	2.2

Northwestern Dent was also crossed with an F_4 W-R segregate from the original cross of Bloody Butcher with W-W, and F_1 was out-crossed with an F_4 W-W segregate of the same original cross. The data obtained are given below.

Table 4.

	Cob	0	1	2	3	4	5	6	7	Total	Mean
C-W/W-R	{R	41	24	16	27	23	26	3	2	167	2.5
	{W	--	--	4	24	18	22	9	1	78	4.1
C-W/W-R W-R	{R	60	9	--	--	--	--	--	--	69	.13
	{W	2	10	24	54	11	1	--	--	102	2.6

The two crosses behaved essentially alike. There was some departure from 3:1 and 1:1 ratios for cob color. The striking features of these records are (1) the absence of the W-W color class in F_2 and the near absence of it in the out-cross to W-W, (2) the relatively few ears and low grade of the C-R class in the out-cross, and (3) the higher mean grade of white cob than of red-cob ears in both F_2 and the out-cross. Thus, in the Northwestern Dent crosses pericarp color, particularly of the higher color grades, tends to be associated with white cob rather than with red cob the reverse of that in the Bloody Butcher crosses. In short, the tendency is to maintain the parental associations of cob and pericarp colors.

Crosses of C-W with W-R, not involving Northwestern Dent but rather C-W and W-R segregates from the original crosses of Bloody Butcher, C-R, with W-W inbreds, have given results wholly unlike those in which Northwestern Dent was used as the C-W parent. The available data are given below.

Table 5.

	Cob	0	1	2	3	4	5	Total	Mean
C-W/W-R	{ R	15	15	17	27	20	6	100	2.4
	{ W	12	4	5	12	1	--	34	1.6
C-W/W-R W-R	{ R	20	16	20	16	--	--	64	1.6
	{ W	24	12	14	--	--	--	50	0.8

Here again cob color segregated normally. The striking features of these data are (1) the relatively high frequency of the W-W class--all but absent in the Northwestern Dent crosses--(2) the high frequency of the C-R class in the out-cross, and (3) the higher color grade of red-cob ears. In short the behavior of these crosses of C-W/W-R, in both F₂ and the out-cross generations, was much less like the behavior of crosses of the same color types when C-W came from Northwestern Dent than like the cross of C-R/W-W when C-R came from Bloody Butcher.

Eight F₃ cultures have been grown from the three color classes, C-R, C-W, and W-R, obtained in F₂ from the cross of Northwestern Dent, C-W, with an inbred W-R. The results are given below.

Table 6.

Cob F ₂ Color	Pericarp grade	F ₃ progenies										Mean grade
		Cob Color	0	1	2	3	4	5	6	7	Total	
R	0	R	20	--	--	--	--	--	--	--	20	0
R	2	R	--	1	7	6	3	--	--	--	17	2.6
R	3	{ R	4	2	1	2	8	2	--	--	19	2.7
		{ W	--	--	--	--	11	4	1	1	17	4.5
R	4	{ R	3	3	1	1	10	1	1	--	20	3.0
		{ W	--	--	--	1	--	6	1	--	8	4.9
R	5	{ R	--	--	3	3	1	3	1	--	11	3.6
		{ W	--	--	--	--	1	1	3	--	5	5.4
W	3	W	--	--	3	17	15	2	--	--	37	3.8
W	6	W	--	--	--	--	4	3	23	5	35	5.8
W	6	W	--	--	--	--	3	10	13	3	29	5.6

As in F_2 , the pericarp-color grade is higher when associated with white than with red-cob; and as in F_2 , the W-W class did not occur. In one case the F_2 recombination class C-R apparently bred true in F_3 for the presence of both cob and pericarp color. It is evident that diverse intensities of pericarp color can be isolated by inbreeding and selection when Northwestern Dent is involved in crosses with colorless pericarp just as is true of Bloody Butcher crosses as reported in News Letter 17 (1943).

From this report and earlier ones, it can be said that the intensity of white-cap red pericarp of such maize varieties as Bloody Butcher and Northwestern Dent and of their crosses with colorless-pericarp strains, is influenced by genes whose action is like that of genes conditioning other quantitative characters. It can also be said that some of these genes are linked with the gene for red or white cob.

To assume that some of the effective genes of Bloody Butcher are represented by ineffective alleles in Northwestern Dent and that the reverse is true of other such genes, and further to suppose that some of them are more closely linked with the cob-color alleles, is of little help without the added assumption of interaction of some intensity genes with red cob and of others with white cob. On such assumptions it might be expected that an F_4 C-W individual from a cross involving Bloody Butcher would have at least some of the genes of Bloody Butcher with the same linkages and interaction with red cob as in Bloody Butcher. Such C-W plants might then be expected to behave differently in crosses with W-R from that of the C-W plants of Northwestern Dent. It is not worth while at the present stage of the study to go into further detail about this complex and somewhat hazy hypothesis. The principal thing to be said in its favor is that it seems amenable to experimental genetic test.

2. Linkage of 4-row ears. Some years ago, I obtained results suggesting that a gene for the 4-row type of ear is in chromosome 6 well to the right of Pl. Four-row cultures were, therefore, crossed with 8-row translocation 6-10a. Y y and Pl pl were also involved. Backcross progenies were grown last summer. There was marked deficiency of 4-row plants as has been observed frequently before in dealing with this character. From a total of 295 plants of the backcross, the following per cents of recombination were found.

Y-Pl	29.5	Y--4-row	41.7
Pl-T	34.2	Pl--4-row	44.7
Y-T	49.5	T--4-row	51.2

From these results it is clear that, if a gene for the 4-row condition is in chromosome 6, its locus is to be sought to the left of Y rather than to the right of Pl.

R. A. Emerson

3. Among the seed stocks belonging to the late Dr. A. C. Fraser were several noted as "segregating for w and l." Seed from a few of these cultures was planted in the greenhouse for student use and they were found, without exception, to be segregating for a dwarf as well as for w or l. The dwarf was later identified as pigmy and the white seedling as wl. Lebedeff, News Letter of March 6, 1938, reported 4.8% recombination between w and py, assuming one w py, none of which were actually found. Among 413 seedlings we likewise found no w py plants, further indicating the close linkage between these loci.

	<u>++</u>	<u>+ py</u>	<u>w +</u>	<u>w py</u>	<u>Total</u>
$\frac{+ \text{ } py}{w \text{ } +}$	212	98	103	0	413

w - py 10.1 % (assuming 1 w py)

The origin of the luteus in this material is unknown. There is no record of outcrossing and, so far as we can determine, it first appeared in S₄ of the cross +/w x py/py. Whatever luteus this may be, it is also linked with pigmy, as indicated by the following data:

	<u>++</u>	<u>+ py</u>	<u>l +</u>	<u>l py</u>	<u>Total</u>
$\frac{+ \text{ } py}{l \text{ } +}$	635	253	292	2	1182

lx - py 9.2 %

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Heterosis, grain yield. For homozygous parents and linear interaction of non-allelic genes, in the notation of Fisher et al Genetics 17:107, 1932, d is (AA-aa)/2, h is the deviation of aa from the midpoint between aa and AA.

$$P_1 = 2n_1d + R$$

$$P_2 = 2n_2d + R$$

$$P = 2nd + 2R$$

$$F_1 = n(d + h) + R$$

$$F_2 = n(d + \frac{1}{2}h) + R$$

$$F = 2nd + 3/2nh + 2R$$

$$B_1 = \frac{1}{2}n(d + h) + n_1d + R$$

$$B_2 = \frac{1}{2}n(d + h) + n_2d + R$$

$$B = 2nd + nh + 2R$$

ϕ is the phenotype, n is number loci heterozygous in F_1 , R is the least homozygote available by segregation.

Analysis of data

Maize yield			Tomato, Powers ³		
Neal ¹	Lindstrom ²	Danmark x Height	Red Current	Johannis.x Fruit wt.	Red C Fruit wt.
Estimates of 2nh			(All records per cent of F_1)		
4(F_1-F_2)	148.1	136.8	76.0	+ 7.2	+ 36.0
(2 F_1-P)	124.4	127.6	58.5	- 751.7	- 625.1
2(2 F_1-B)		113.2	62.8	- 241.6	- 228.8
2(2 F_2-P)	130.3	118.4	41.0	-1510.6	-1486.3
4/3($F-P$)	126.4	124.5	52.6	-1004.7	- 845.0
4($F-B$)		89.6	49.6	- 490.4	- 493.6
2($B-P$)		142.0	54.2	-1261.8	-1021.5
Mean 2nh	132.3	121.7	56.4	- 750.5	- 666.3
($F_2-\frac{1}{2}B$)		- 5.9	- 3.3	- 67.5	- 67.3
P	75.6	72.4	141.5	950.7	836.6

¹J.A.S.A. 27:666, 1935. ²Proc. 7 Int. G.C. ³J.A. Res. 63:149, 1941.

The close agreement of Neal's and Lindstrom's data in the above analysis seems to indicate strongly that grain yield is a function of heterozygosis. For any locus, $(aA-aa) - (AA-aA) = (h+d) - \frac{1}{2}d - (h+d) = 2h$. The interval from the least homozygote to the heterozygote minus the interval from the heterozygote to the top homozygote is 2h for one locus or 2nh for n loci, if h and d values are essentially the same for all loci.

For all values of h or h/d (any degree of dominance) the 7 estimates of 2nh (table) are a homogenous set, except for non-genetic fluctuations. Heterogeneity indicates interaction of non-alleles.

The three quantities, $(P = 2nd+2R) > (F_1 = nh+nd+R) > 2nh$ must lie in that or the reverse order with each interval in any case equal to $\frac{1}{2}n(h-d)-R$. If $h=d$ (dominance complete) the intervals are estimates of R. On that assumption the mean estimate of R for the two maize records is minus 26.5% F_1 . If R cannot be negative the minimum estimate of R equal zero provides the minimum estimate of h equal 1.7d.

The top homozygote is (P-R). For these records it cannot be estimated larger than 74% F_1 if negative R is to be avoided.

The data on tomato weight and estimates of $2nh$ from them may seem to suggest a complication of interactions, although the two sets of $2nh$ are quite similar. It is proposed to separate allelic from any regular non-allelic interaction graphically. The points P_1 , B_1 , F_1 , F_2 , B_2 and P_2 are plotted with the scale on the ϕ axis being that of the actual data and on the x axis that of allelic but no non-allelic interaction. Lay off a wide interval from P_1 to P_2 on the x axis. Trial positions of F_1 may then be taken with F_2 midway between F_1 and the mean of parents and each backcross midway from F_1 to the recurrent parent. The best trial position of F_1 should be $2(F_1 - F_2)$ from the mean of parents in the direction indicated by the data, since F_1 and F_2 have the same gene number and their comparison will be least affected by non-allelic interaction. If the 6 plotted points do not seem to lie on a smooth curve F_1 is to be shifted right or left with F_2 and backcross shifts being $\frac{1}{2}$ of the F_1 shift until the best fit to a smooth curve is obtained. The curve presumably represents regular non-allelic interaction or regular interaction with environment. Allelic interaction is evident in the 7 estimates of $2nh$ which should be a uniform set.

In this way, close fits to smooth curves were obtained with Power's data on the crosses Danmark x Red Current and Johannisfeur x Red Current with F_1 s just slightly to the right of the parental midpoint towards heavier fruit. The curves lie between $\phi = kx^3$ and $\phi = b^x$ over most of the range. Both agree closely with the hypothesis of very slight dominance of heavier fruit and strong, regular interaction of non-alleles. The interaction may of course be little more than the cubic relation of weight or volume to linear dimension.

A slightly poorer fit was obtained for Johannisfeur x Bonny Best but the same dominance bias and interaction is evident. The two records on Danmark x Johannisfeur did not provide consistent solutions, perhaps because the parents are too close together. That difficulty would always appear with yield records on inbred maize.

Complementary interaction is not regular in the above sense. It might become evident in the $(F_2 - \frac{1}{2}B)$ comparison and in aberrations from regular interaction in the above graphical analysis. With 2-factor interaction, F_2 is $9/16$ and $\frac{1}{2}B$ is $8/16$ of the interval from $\frac{1}{2}P$ to F_1 ; both are $8/16$ without interaction. There is no evidence of complementary interaction as a factor of heterosis of maize yield or of tomato plant height. There seems to be no evidence for complementary interaction for tomato weight except in the cross Johannisfeur x Bonny Best. If the curve for that cross is plotted by neglecting the F_2 to obtain the best fit with F_1 and backcrosses the F_2 deviation from the curve is large and positive which may indicate complementary interaction for heavier fruit. Plotting $3\sqrt{\phi}$ or $\log \phi$ might bring the complementary interaction out more clearly.

The reader should be warned that application of the above graphical analysis to data involving little or no non-allelic interaction and strong interaction of alleles as in tomato plant height may produce a straight line with the 6 values spaced the same on both axes or a smooth curve through P_1 , B_1 , $F/2$, B_2 and P_2 . In the latter event the six values will agree with the hypothesis of no allelic interaction on the x axis. The factor of curvature here is h . I do not now have the function.

For linear interaction of non-alleles, theoretical regressions in F_2 and backcross of ϕ on x (gene number) are:

$$F_2; \phi = \frac{-hx^2}{2n-1} + \frac{(2n-1)dx + 2nhx + R}{2n-1}, \quad d\phi/dx = d + \frac{(2n-2x)h}{2n-1}$$

$$B_n; \phi = \frac{nd + (n-2n_b)hx}{n} + \frac{2n_b h^2}{n} + R, \quad d\phi/dx = d + \frac{(n-2n_b)h}{n}$$

n is the number of loci heterozygous in F_1 ; n_b is the number of n loci fixed AA in the recurrent parent.

These equations seem to be mainly useful for the solution of theoretical problems. For example, the backcross distribution is not skewed by any degree of dominance even though the recurrent parent is fixed AA at all n loci, ($n_b = n$). The slope is then $(d-h)$ or zero if $h = d$. If $h > d$ the slope is negative -- ϕ decreases as the number of plus genes increases. If n_b is zero the slope is $(d+h)$ -- positive unless h is negative and greater than d .

F_2 regression is a second degree parabola with slope a function of $-2hx$. The F_2 distribution is skewed by dominance. The familiar case ($h = d$) involves the left branch of the parabola from $(0, R)$ rising with decreasing slope to the vertex at $(x = 2n - \frac{1}{2})$, then dropping slightly to $(x = 2n)$. This function may be employed with the normal frequency table to construct a theoretical distribution for any number of loci and any degree of dominance to show that maximum skewness is reached when $h = d$; and that skewness then decreases with increasing h . The demonstration is facilitated by working with one pair of genes. Thus if $A'A'$ equals AA, and $A'A$ is some greater value, d is zero and h is relatively large. The F_2 , $(\frac{1}{4} A'A' + \frac{1}{2} A'A + \frac{1}{4} AA)$ becomes $(\frac{1}{2} A'A', AA + \frac{1}{2} A'A)$. This distribution or the product of any number of such distributions is symmetrical. If d is now allowed to take increasing positive values, skewness increases up to $h = d$. East's alleles of divergent function would not intensify skewness of F_2 .

The conclusion of $h > d$ for maize yield is supported by failure of mass and ear row selection, by failure of synthetic combinations of selected inbreds, by superiority of hybrids of inbreds

of diverse origin, and by the success of modern maize breeding itself. If h is not greater than d , mass or ear row selection will probably continue to surpass present maize breeding technic, because of more frequent recurrence of selection. But if $h > d$, present technic is the only method so far tried which should effect appreciable improvement. No degree of allelic interaction will confuse selection among F_1 hybrids of homozygous lines. However, selection favoring the heterozygote loses efficiency rapidly. It is questionable if the expectation of continuing success with present technic can be supported in Mendelian theory.

Selection may be measured by the deviation of the mean of a selected group from the original mean in terms of the standard deviation of the original. Thus "student" noted selection effects of 12 and 7 sigma for high and low oil in the Illinois experiments. If the selected group may be represented by a tail of the normal area cut off above $x = t$, and the mean of the tail is s ; $s = (\text{ordinate at } t) / (\text{area beyond } t)$, or (P_t) . Then $1/P_t$ is the number of individuals from which selection of the top one may be expected to effect a selection differential of the given value of s . The highest value of s calculable from a 15-place table of areas and ordinates of the normal curve, (W.P.A. City of New York) is 8, for which $1/P_t$ is 222,222,000,000,000. This is roughly 2000 times the number of maize plants grown in the world in one season. That the low oil result ($s = 7$) might have been obtained by selection among 400,000,000 homozygous lines is plausible. The high oil result ($s = 12$) is 4 billion million times as difficult. Selection of the top 10 from 26 provides an s of one in the absence of gene interaction and environmental effects. Eight recurrences of such selection will effect an s value of 8 if variability is maintained as it was in the selection for oil. A total of 208 plants is required. From this viewpoint the oil selection results do not seem improbable as the work was done; they do seem very improbable in the face of much inbreeding.

The s value of the top one of 11, 185 singlecrosses from at least 150 inbred lines is about 4. This might be a yield increase of about 40% over original stock. The genetic variance of singlecrosses is the same as for single plants of original crossbred stock. Sigma in this case is then 10% of the original mean yield. This seems a fair estimate of the present Florida situation. The problem now is how much effort will be required for further gains. If each cycle of inbreeding must begin at the same level as the first, as indicated by the yield of synthetic combinations of selected lines and nearly all other available evidence, it will be necessary to identify the best single cross among 1,300,000 from 1600 homozygous lines to effect a further improvement of 10%. Gaining 10% again beyond that will be truly difficult, even though the genetic variation may remain unimpaired in the process as suggested by oil selection results.

A breeding technic has been proposed to deal with the case $h>d$, Hull, Recurrent Selection for Specific Combining Ability in Corn. J.A.S.A. in press. The method is recurrent selection in a crossbred lot for combining ability with a specific homozygous line. Selection is among testcrosses of single plants of the crossbred lot to the homozygous tester line. For any locus heterozygous in the crossbred lot and aa in the tester the testcrosses are: aa , $(aa+aA)/2$, and aA , or if the tester is AA they are: aA , $(aA+AA)/2$, and AA . The three testcrosses are separated by equal intervals, $(d+h)/2$ in the first case and $(d-h)/2$ in the second. The essential point is that the three values are equally spaced as would be the three genotypes in a crossbred population without dominance. This type of selection avoids the confusion of dominance or allelic interaction even though $h>d$. The price is some loss of variance. It also allows maximum frequency of recurrence of selection. Maximum frequency of recurrence with respect to resistance to insects and diseases as well as to yield and any other desirable characters would seem to be obtained by simultaneous selection.

Tomato weight and height have been included for contrast with maize yield. Estimates of $2nh$ involving $(-B)$ are smaller than those involving $(-P)$ for both maize yield and tomato weight. B values might suffer less distortion from non-allelic interaction than P values since the former are nearer the center. The slightly excessive value of B in Lindstrom's data may indicate nothing more than a little heterozygosity remaining in the parent lines. Strong allelic interaction is indicated for maize yield. Tomato weight records indicate very slight allelic interaction but strong non-allelic interaction. Both the maize yield and tomato weight situations seem improbable. If the tomato weight interaction is the cubic relation of volume to linear dimension, why does not this function appear in the relations of aa , aA and AA at one locus? Why would it not appear in the maize yield between non-allels? Why does $h>d$ appear only in grain yield of maize; not in components, e.g. ear length and diameter, plant height, stalk diameter etc.? Tomato height in F_1 exceeds the greater parent but not the sum of parents (P). There is no evidence here of $h>d$ and slight evidence of non-allelic interaction.

The enormous selection intensities available by properly controlled recurrent selection provide a tool for investigation of physiological limits, limits of recombination, and perhaps detection of aggregates of natural or induced mutations in a group of numerous small genes.

Appendix - January 10, 1945: Hayes et al, J.A.S.A. 36:998, 1944; data on synthetic, mean of parent lines and mean F_1 . From F_1 minus synthetic the estimate of $2nh$ is 160% F_1 . The $(2\bar{F}_1 - P)$ estimate of $2nh$ is 127% F_1 . If $h = d$, and $R = 0$, then $F_1 = 2nh$. Decline from F_1 to F_2 or synthetic is $2nh/2N$, where N is number of lines. On the foregoing assumptions, expected decline of Hayes' synthetic is 100/16 or 6.25 % F_1 . If R is 20 % F_1 , expected decline of synthetic is 5 % F_1 .

The actual decline of 10% F_1 , may be evidence of $h > d$, non-allelic interaction, or $R < 0$. Taking $R = 0$, no interaction, then $h = 4d$ for the F_1 - synthetic comparison, and $h = 1.74d$ for $(2F_1 - P)$.

Kiesselbach, J.A.S.A. 22:614, 1930; F_2 and F_3 of 21 single-crosses, $h = 1.98d$.

Richey et al, J.A.S.A. 26:196, 1934; F_2 10 double crosses, $h = 1.55d$.

Neal, loc. cit., F_2 10 double crosses, $h = 1.72d$.

If R is some positive value all of the above estimates of h must be revised upward.

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1. Pod corn. The sterility of homozygous pod corn is largely due to an excessive vegetative proliferation which may take various forms. Ts₅ is an important modifier to Tu; it brings Tu under "control" and prevents some of the unrestrained proliferation which characterizes Tu under some conditions.

Tu can also be brought under control by various unidentified genes in the modifier complex. It can be assumed that Tu is frequently a monstrous character because it is the product of the "wild" gene superimposed upon modern varieties which lack the modifiers which in wild maize must have kept the character under control. If this assumption is sound then modifiers of Tu should be particularly abundant in primitive varieties of maize. The nearest approach to "primitive" maize which we have so far discovered is the maize of the Guarany Indians of Paraguay. When this is crossed with Tu and the hybrid repeatedly backcrossed to Guarany, the glumes of the Tu tu plants are decidedly reduced. Other stocks are now being tested for their modifier complexes with regard to Tu.

We now have a homozygous true-breeding pod corn. Tu Tu plants with both staminate and pistillate fertility were found some years ago but such plants are very difficult to self because of the long interval between silking and anthesis. Selfing, however, has finally been accomplished.

The hybrid of pod corn and Guarany mentioned above has unexpectedly furnished a most striking demonstration of the real nature of the ear of maize. Under certain conditions Guarany maize has a tendency to produce a partially indeterminate ear, which once protruding beyond the husks elongates considerably. Tu accentuates this

tendency. During the past year we have obtained ears which are normal at the base but enormously elongated at the tip. This "stretching" shows that the ear of maize is fundamentally a simple spike with pairs of spikelets in whorls at the nodes of the rachis.

2. Maize-teosinte crosses. Studies of the genetics of maize-teosinte crosses have been greatly facilitated by the development of a stock with a marker gene on each of nine chromosomes, ten if the other parent is pr. (bm² lg a su Pr Y/y gl i wx g) This stock has been inbred and is uniform. Needless to say it is weak, so weak that most of the plants are barren and many do not shed pollen. But difficult as it is to maintain the stock is extremely valuable. It imparts considerable vigor to its crosses and it permits the investigator to control nine of the ten chromosomes in a single cross.

This stock was crossed with two varieties of teosinte, Durango and Nobogame. F₂ results are shown in the accompanying table. In the Nobogame cross the nine marked chromosomes segregate independently of each other as would be expected if no translocations, "sticky" chromosomes or other complicating factors are involved. In the Durango cross there are two significant deviations, one in the direction of linkage between Su and J and another indicating "repulsion" between Wx and Gl. There are additional deviations approaching statistical significance in the Durango cross.

In addition to the nine marker genes the plants in both crosses were scored for five characteristics, in which maize and teosinte differ. One of these, a red spot at the base of the staminate glumes, Bs, is also found in some maize varieties, particularly South American and is not regarded as an important character from the standpoint of differentiating maize and teosinte. The remaining four are characters involved in interspecific differences. They are (with the teosinte characters listed first):

1. Tr Two-ranked vs. many-ranked ear or central spike.
2. Pd Single vs. paired spikelets.
3. Sd Strong vs. weak response to length of day.
4. G. S. (Glume Score) Prominent horny glumes vs. inconspicuous membranous glumes.

Langham's symbols for the first three characteristics are used although the characters involved did not prove to be simple monofactorial in their inheritance in these crosses. All of these characters showed linkage with each other and all but the second showed linkage with one or more of the nine marker genes.

3. Chromosome segments from Florida teosinte. The segments of chromatin or blocks of genes which distinguish Florida teosinte and maize have been transferred by repeated backcrossing to a uniform inbred strain of maize. Two of these have now been crossed with the nine-gene multiple tester stock previously mentioned and backcrossed

to the multiple recessive. Here we are studying only the dominant effects of the chromatin segments from teosinte.

One of these segments proved to be linked with A on the third chromosome the other with Su on the fourth. In both cases the segments are somewhere near the center of the chromosome, the segment on the fourth includes the Su locus, the segment on the third shows approximately 25% crossing over with A, which is known to be near the end of the chromosome. Both segments have the same kinds of effects. Both reduce the number of rows of grain, the size of the seed and affect the development of the pistillate glume structure.

The segment on the third chromosome is usually inherited intact but that on the fourth is frequently broken as a result of crossing over. Parts of the segment have the same general effects as the entire segment, but in a smaller degree.

It is quite possible that the problem of inheritance of row number in maize is complicated by small segments of this kind originally derived from Tripsacum through admixture with teosinte. The crosses of Nobogame and Durango teosinte previously mentioned showed that genes involved in the difference between the two-ranked and the many-ranked condition occur on at least seven of the nine chromosomes tested. These are probably the same kind of genes which account for differences in number of rows of grain in some varieties of maize.

Summary of Linkages in Teosinte Crosses

Nobogame x Multiple Tester - F2														
	Bm ₂	Lg	A	Su	Y	Gl	J	Wx	G	Tr	Sd	Pd	G.S.	Bs
Durango x multiple tester - F2	Bm ₂	-	-	-	-	-	-	-	-	+	-	-	-	-
	Lg	-	-	-	-	-	-	-	-	+	-	-	-	+
	A	-	-	-	-	-	-	-	-	I	-	-	I	-
	Su	-	-	-	-	-	-	-	-	-	-	-	+	-
	Y	-	-	-	-	-	-	-	-	+	-	-	+	-
	Gl	-	-	-	-	-	-	-	-	I	-	-	+	-
	J	-	-	-	+	-	-	-	-	+	-	-	+	-
	Wx	-	-	I	-	+	-	-	-	+	-	-	-	I
	G	-	I*	-	-	-	-	-	-	-	I	-	I	-
	Tr	-	+	+	+	-	-	+	+	-	+	+	+	+
	Sd	-	-	-	-	-	-	I	-	+	+	+	+	-
	Pd	-	-	-	-	-	-	-	-	+	+	+	+	-
	G.S.	-	-	+	+	-	-	+	+	+	+	+	+	-
	Bs	-	+	-	-	-	-	-	+	+	+	-	-	-

+ = Linkage

I = Indication of Linkage

- = Independent Inheritance

* = Deviation in Direction of Repulsion

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1. Glossies. Glossy S-2 (one of Stadler's mutants) is the same as gl₆, leaving gl S-1 and gl S-3 which are not completely tested.

2. White Cap. Additional backcross data show linkage between W^C and T₁-9b (31.3% recomb. in 208 plants); W^C and T₁-9c (26.0% in 127 plants) and new data show no linkage with T₁-10a (149 plants). The breaks in chromosome 1 are: .6 long arm, .6 short arm, and .4(-) long arm respectively. The breaks in chromosome 9 in the first two interchanges are at .5 long arm and .2 long arm respectively. These data indicate chromosome 1 is not the one carrying white cap. A previous test with 9-10a (break at .3 long arm of 9) had shown no positive evidence of linkage from which it was concluded that W^C is in chromosome 1 (1944 news letter). Closer examination of these data shows $35.4\% \pm 5.1\%$ recombination in one culture, independence in a second, while the combined results do not deviate significantly from 50%. In a backcross linkage test on 190 plants there was no linkage between W^C and P. In the same culture f was segregating 3:1 with no indication of linkage. W^C, therefore, is probably not in chromosome one, but in chromosome 9. If so it is probably in the long arm since a test with waxy showed no linkage (1944 news letter).

3. Midcob color. Some evidence of linkage between red midcob color and yellow endosperm was obtained, although the results were complicated by the presence of both W^C and pale yellow endosperm. Certain cultures segregate clearly 3 red: 1 colorless midcob; others show an excess of the colorless midcob class.

4. Miscellaneous. The character brown midrib-3, bm₃, is closely linked with sugary-1. F₂ repulsion data were: 111 Su Bm, 63 Su bm, 57 su Bm.

Vivipary-5 (vp₅), reported by Lebedeff (coop. letter of March 5, 1940, page 14) as closely linked with yellow (probably Y) is not linked with the Y₁ in chromosome 6; since vp₅ and ms₁ segregate independently. On ears segregating 9 yellow : 7 white or pale yellow, vp₅ showed about 1% of recombination with yellow.

Another vivipary from C.M. Woodworth which has not been tested against vp₅ shows close linkage with yellow on ears segregating 3 yellow : 1 white.

Before the ears had dried in the field, viviparous seedlings from both sources were transferred to soil in the greenhouse. In all cases they proved to be albinos. Although many of these had shown some pale green color underneath the husks, this color soon disappeared.

Piebald-5 (pb5) was reported by Lebedeff in the same news letter to be linked with Y and Pl. This is confirmed by a test which shows close linkage with ms1, and also by the independent segregation of pb5 and vp5.

I have been unable to identify the zg3 character obtained originally as Co 306-1 (x) - A B pl Y zg3.

5. Partial sterility studies. One case with about 75% pollen abortion and a ring of 8 chromosomes (originated by x-ray treatment of a homozygous 5-7 interchange stock) was identified by Mr. Lazaro as involving chromosomes 1,5,6 and 7. In new data from crosses of normal x 75% sterile plants, the offspring included 75% sterile:semisterile:normal::273:71:181. Six different semisterile plants derived from the ring-of-8 were shown by him to have a single ring of 4 chromosomes one of which was number one, while in no case was number 6 involved.

A stock homozygous for the interchanges involved in the ring-of-8 (1-5-6-7) has been established.

6. Chromosome disjunction. In an abstract (Records Genetics Society-1944, p, 14) it was reported that chromosome disjunction in a plant heterozygous for interchange T5-6c was markedly changed when the position of the chromosome 5 centromere was shifted nearer the center of the cross by the presence of a homozygous inversion in chromosome 5. It was also reported that the amount of cytologically observed crossing-over when the inversion was heterozygous was different depending on whether the inversion was present in the interchanged chromosome 5 or in the non-interchanged 5. Cytologically the pairing configurations in the two cases should be similar. It was thought possible that some additional change might have accompanied the crossing-over by which the inversion was introduced into the interchanged chromosome 5. Accordingly a prophase study of the following homozygous stocks has been made: inversion in chromosome 5 T5-6c, and T5-6c plus inversion. Fortunately one of the breaks in the inversion and in T5-6c was in a heavy chromomere region, while the second was in a region with small chromosomes. Positions of breakage and rearrangement could be clearly recognized. The stock combining both also appeared to have the exact morphology expected. The differences in crossing over mentioned above appear to result from some other cause.

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Maize in Mexico. Maize in Mexico may ultimately be of practical importance to the U. S. corn belt because it constitutes such a reservoir of genic variability. We may also find that we must study Mexican varieties in order to understand our own, since our ultimately came from the south. This will be rather difficult since the whole pattern of variation in Mexican maize is so different and so much more complex than that in the U.S. The over-all morphological diversity in the maize of a single Mexican town may be as great as in all of the U.S., yet in another Mexican region 300 miles away the varieties may be entirely different but quite as varied. These regional differences are due in part to the great differences in altitude, temperature, rainfall, and growing season which characterize Mexican agriculture.

During my six months in Mexico I attempted to make a reasonably complete survey of the regions around Guadalajara (Jalisco, western Mexico) and Mexico City, with scattering collections through the intervening area. A random sample of 25 ears was taken from each field or corn crib and 15 measurements were made on each ear. A few collections have been examined cytologically for knob number and tested genetically for c, r, and pr. The following generalizations are already established.

1. Maize of western Mexico. In spite of much variation in color, row number, and kernel size, the maize of western Mexico is prevaillingly long and slender-eared, tapering somewhat to the base and long and irregularly to the apex. Its husks are so tight that there are usually conspicuous striations running lengthwise of the ear. The row number is commonly 8 to 12, the kernels are frequently broad, seldom pointed, and the denting is slight or none. The plants are strong-rooted and stiff stalked. Chromosome knob numbers are high (10 or more) and the knobs are large. The recessive genes r, c, and pr are common.

2. Maize of the Mexico City Region. The maize of this region is prevaillingly short-eared and sharply and regularly tapering to the apex. Row numbers are usually above 12, the kernels are more or less pointed and are frequently strongly dented. Chromosome knobs are 0 or a very few. The plants are shallow rooted, the tasselbranches few in number and the leaves broad.

In the intervening area between Mexico City and Jalisco an intermediate and variable type is commonly grown. This is particularly true of the Mexican corn belt (the "Bajio"), centered about the state of Guanajuato.

A few outstanding varieties have wide distribution and deserve special attention.

1. Mai'z dulce, the sweet corn of western Mexico is in general unlike the corn of that region and shows striking similarities to similar sweet varieties in highland South America. Dr. Kelly and I have published a detailed report on it. (Ann. Mo. Bot. Gard. 1943).

2. Cachuzintle, a large kernelled white, flour corn grown in the region around Mexico City and southward. Its plant type is strikingly unlike the other maize of that region. It is "popped" by cooking in rapidly boiling water.

3. "Elote" corns with colored aleurone. Throughout all these regions varieties with colored aleurone (both Pr and pr) are almost universally grown. They are said to be sweeter than the other varieties and are favored for green corn on the cob (elote) and parched cornmeal (pinole). Some of them have fine wrinkles and look as though they might carry su and an inhibitor.

4. Popcorns. There are at least 3 popcorns in Mexico if we include cachuzintle under that name. The other two are morphologically very different from each other in everything but popping ability. They are: Mai'z reventador, the Jaliscan variety for which I have recently (Ann. Mo. Bot. Gard. 1944) published a detailed report and the rice pops of Toluca and other towns near Mexico City. The latter are similar to the semi-pointed dent corns of the same region in plant and tassel characters and are grown inter-mixed with them.

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1. Gamete Selection in Corn Breeding. The method of corn improvement commonly known as "selection in self-fertilized lines" has been remarkably effective in the development of types of corn far superior to any previously existing variety in yield and in other agronomic characters of practical value.

The general experience of corn breeders and the results of the experimental studies of breeding methods which they have made indicate that, if this job were to be done over, it would be possible to make comparable advances at a much smaller cost in time and labor. The chief results of the method experiments, as related to yield improvement, may be summarized as follows:

- (1) Visual selection for yield is practically ineffective. The extent to which a plant of given genotype will contribute to yield in hybrids can only be determined by yield testing of its hybrid progeny. The factor limiting the scope of breeding operations is the number of items which may be adequately tested for yield.

- (2) The combining value of a given genotype varies considerably in combinations with different genotypes. General combining value may be tested effectively in practice by crosses on mixed populations.
- (3) The inheritance of yield genotype is in general in agreement with expectation based on the hypothesis of complementary dominant favorable factors.
- (4) There is little or no advance in yield genotype in the course of inbreeding and selection as ordinarily practiced in the production of inbred lines. This fact, convincingly demonstrated by Jenkins, is the basis for current attempts to improve the efficiency of the breeding technic, for it shows that the method owes its success not to selection in self-fertilized lines, but to the unrecognized differences in genotype of the foundation plants.

Jenkins' results suggest the possibility that an appreciable fraction of the individual plants in open-pollinated varieties may be as high in yield genotype as the best present inbred lines. Obviously, the identification of these plants near the beginning rather than near the end of the breeding operations would make for greater efficiency, for it would concentrate the analysis upon populations with the highest content of desirable genotypes. In the few outstanding selected strains it would be feasible to use test-controlled selection in the first selfed generation, where genetic variability is at its maximum. Such selection might reasonably be expected to accomplish further improvement in yield.

This is an effective and practicable method for the further sampling of the open-pollinated varieties. It is not widely used in corn breeding at present, chiefly for these reasons:

- (1) The frequency of high yield genotypes among the plants of open-pollinated varieties is low enough to make their identification much less economical than that of comparable genotypes in populations of various types which may be produced by the use of the highly improved lines now at hand.
- (2) The exceptional genotypes identified are virtually unselected as regards characters other than yield. Some of these characters are very important in practice, often more important than a considerable increment in yield.

The critical factor determining the practical feasibility of varietal sampling is the frequency in the varieties of genotypes

approximating the yield level of the present elite strains. The limiting data available (all for trials in single seasons) indicate rather high variability in yield genotype among plants of open-pollinated varieties, averaging about 9% of the mean yield after removal of the variance due to experimental error. The distribution of yield level in these populations is normal. The data unfortunately do not show where the present elite lines would fall upon these distribution curves. The general experience of corn breeding in the past 20 years is probably a better basis for estimating the frequency of plants in the foundation varieties which approximate the elite yield level. On this basis a fair estimate of this frequency is 1 or 2 per cent.

Despite its relatively low return, the further sampling of the open-pollinated varieties is essential. The greater part of the hybrid corn now grown is the product of various combinations of about a dozen inbred lines. Each of these represents a single gamete genotype, fixed as a homozygous diploid for controlled combination. These, with the additional lines of promise for further breeding, constitute a minute sample of the gamete populations of the foundation varieties. To confine further breeding to the recombinations of this small group of genotypes is to reduce its ultimate possibilities to an extent which cannot be accurately estimated from available evidence but which must be pretty drastic. Moreover, any new line produced from the recombination of the old lines is limited in its practical use, for no line gives good combinations with lines to which it is related.

Now these varietal populations, in which 1 or 2 per cent of the members reach the elite level, are populations of open-pollinated plants. Each plant represents a random combination of two gametes of the varietal gamete population. The yield potential of the plant is the result of dominant factors contributed by the two parental gametes. The frequency of genotypes of unusually high (or low) yield-potential must be much higher in the gamete population than in the population of open-pollinated plants. In a variety in which plants of yield potential equal to the elite lines occur at a rate of about 1 per cent, gametes of correspondingly high average yield potential constitute almost 10% of the gametic population. This group includes the tail of the frequency curve, and the best 1-2% may be genotypes well in advance of the elite level. Gametes constituting 1% of the population represent a level of yield potential occurring among the open-pollinated plants with a frequency of only about 1 in 10,000. Such genotypes may represent a level of efficiency in grain production which has not been closely approached by selections made from the open-pollinated plants.

The term "yield potential" (YP) as here used refers to the capacity of the genotype for contributing to yield in specific hybrid combinations. Detailed definition and illustration of the concept of yield potential must be omitted here for brevity, but it may be briefly described as follows: The yield potential of a homozygous individual, with reference to any homozygous biotype used as a

tester, is (for given conditions) the excess in yield of the F_1 or test-cross over the tester biotype. The YP of the gamete genotype of this individual is one-half of this value. When the tester is a hybrid or mixed population, the YP of the tested individual is the excess of the F_1 over a hypothetical yield which would be produced by biotypes representing the gamete population of the tester. This quantity is indeterminate, but since it affects all test cross yields equally its determination is unnecessary. In practice, YP with reference to a hybrid or mixed tester may be determined as accurately as to a homozygous tester, since the number of plants of each test-cross required for an adequate yield test is large enough to render negligible any variation due to individual plant variability.

In the absence of direct evidence, it is necessary to make certain assumptions regarding the inheritance of YP. The validity of these assumptions for the present purpose does not require that they be precisely correct in specific instances but rather that they represent correctly the general or average interaction of the factors involved. All assumptions regarding inheritance of YP in this discussion are derivable from two postulates which are in harmony with the evidence now available but which still require direct experimental verification. These postulates are as follows:

- (1) The YP of an individual is the sum of the YP's of its parental gametes.
- (2) The mean of the YP's of the gametes produced by an individual is equal to the mean of the YP's of its parental gametes.

In the initial stage of an isolated corn breeding program, the gamete cannot be made the unit of selection, since there is no homogeneous gamete population with which the varying gametic series may be combined for comparative testing. It is therefore necessary to select among the plants produced by the random combination of gametes of all levels. After an initial series of inbreds distinctly superior to the varietal means has been established, it is possible to use these inbreds in further sampling of the varieties, and in this procedure the gamete may be the unit of selection.

Gamete selection in practice would ordinarily involve two steps:

- (1) The selection, on the basis of outcross yield tests, of individual plants of a variety/inbred population, and
- (2) A similar test-controlled selection in the first generation self-progeny of the outstanding individuals identified in the first step. This would ordinarily be followed by continued selfing, with visual selection, to fix a line homozygous for the desired agronomic characters as well as yield genotype.

For some purposes continued selfing would be unnecessary; notably for the extraction of plants of value in complex crossing. Complex crossing for the extraction of improved lines has been little used in corn breeding, chiefly because of the limited number of good lines available. But homozygosis is not essential in the strains used in complex crossing, and the heterozygous strains identified in the plant selection and gamete selection tests may be used without sacrifice of the established inbreds.

The technic may be illustrated by an experiment now in progress. The variety used is Midland, which has given exceptionally good yields among open-pollinated varieties in central and southern Missouri and in other localities in the southern Corn Belt. The inbred used is WF9, which is outstanding in performance among lines now available in the Corn Belt, though it is a little too early to make full use of the growing season in Missouri. It is one of the parents of U. S. 13(WF9/38-11 x L317/Hy) the hybrid now most widely grown in Missouri.

Each Midland/WF9 plant is selfed and is outcrossed on a tester stock, in this case L 317/Hy. Each outcross tests the yield potential of one Midland gamete added to that contributed by the uniform gametes of WF9. Similar outcross tests on L317/Hy are made for comparison from the line WF9, and from F₁'s of WF9 with various inbreds of outstanding performance in this region.

Any Midland/WF9 plant which excels the performance of WF9 in outcross yield tests under varying and representative conditions represents a Midland gamete superior in yield potential to WF9, in a combination in which WF9 is very effective. The selfed progeny of such a plant provides a population in which further improvement by test-controlled selection should be possible. This selfed progeny is comparable to the F₂ of a cross of WF9 with an unrelated elite line. As compared to such F₂'s it has, in addition to its possible advantage in yield genotype, the merit of avoiding interbreeding of the tested lines. A derivative of WF9 x L317 cannot be used effectively with either WF9 or L317; a derivative of WF9 x Midland can be used with any other line except WF9.

In comparison with selfs of plants selected from the pure variety, the variety/inbred selfs have certain distinct advantages and disadvantages. For brevity the former will be referred to as the plant-selection series and the latter as the gamete-selection series.

The chief advantage of the gamete-selection series is the expected superiority in yield potential of the best individuals in the population, or in the limited sample of the population which may be effectively tested for yield-genotype. It has in addition the following noteworthy advantages:

- (1) A probably greater range of segregation for yield potential in the selfed progeny of the selected individual. This segregation is

the basis for any further improvement in yield which may be made by a second application of test-controlled selection in the selfed progeny of the selected plant. The extent of this segregation is dependent upon the difference in the specific yield-controlling genes contributed by the parental gametes. The yield potential of the selected plant would benefit as much, on the average, from five such genes, each contributed by both parents, as from ten, each contributed by only one of the parents. But the possibility of further improvement in yield potential would come only from the latter.

It would be expected that a self of an outstanding Midland plant, representing a combination of one superior Midland gamete with another, would be heterozygous for fewer yield factors than a self of a Midland/WF9 plant of equal yield potential, representing a combination of a superior Midland gamete with a superior gamete type of unrelated origin. The evidence available is very limited, but indicates that this difference is an important one.

(2) A better opportunity for extracting a line satisfactory in characters other than yield. In a series of Midland selfs, the only selection for such characters previous to yield testing would be that made among the individual foundation plants. It may be expected that the plants of highest yield potential might in many cases be unsatisfactory in other respects. The series of Midland/WF9 selfs is also virtually unselected, but since each plant is heterozygous for the favorable agronomic characters of WF9 it should be possible, in the extraction of homozygous lines from the selfed progeny, to avoid undesirable characters which are not common to the Midland selection and to WF9. This advantage will vary with the line used, but in major characters such as strength of stalk, for example, any elite line selected for use in this type of experiment would provide some insurance against the weaknesses likely to be met within unselected genotype of the open-pollinated varieties.

The chief disadvantages of the gamete-selection series are the following:

(1) In gamete selection it is impossible to fix the genotype selected from the variety; it can be used only to extract a combination of this genotype with some other genotype chosen in advance, (such as the WF9 genotype in the present example). The line ultimately derived from this combination is restricted to use in crosses not involving WF9. In plant selection a new line is derived which may be combined with other lines without restriction, and which may be crossed for further improvement with lines chosen after the properties of the selected Midland line are known.

(2) In yield testing to compare the value of the Midland gametes, the gametic genotypes compared represent only half of the genotype of the plants which are tested; in plant selection the genotypes compared are the total genotypes of the plants tested. A more accurate yield test is therefore required to detect significant

differences in the gamete-selection series. The accuracy of yield tests is limited, and this imposes a minimum limit to the difference in yield potential which may be used in breeding. Furthermore, increased accuracy is expensive, and reduction of the standard error to one-half requires yield tests about 4 times as extensive. If differences only half as large are to be detected, only about one fourth as many items could be tested with equivalent outlay.

The gamete-selection series would involve smaller differences than the plant-selection series, but the differences to be expected are considerably more than half as large. The net variability of the outcross test yields, after removal of the superimposed variability due to experimental error, is the measure of the yield potential of the plants tested. The yield potentials of a series of open-pollinated Midland plants are the sum of the yield potentials of the male and female gametes combined. These may be represented as follows:

YP of Male Gametes	$A \pm \sigma_A$
YP of Female Gametes	$B \pm \sigma_B$
<hr/>	
YP of O. P. Plants	$(A + B) \pm \sqrt{\sigma_A^2 + \sigma_B^2}$

In wholly unselected series, A and B are equal and the yield potential of the open-pollinated plants is $2A \pm \sqrt{2} \sigma_A$

The yield potentials of the F_1 plants of WF9 x Midland would be as follows:

YP of Male Gametes	$A \pm \sigma_A$
YP of Female Gametes	$C \pm \sigma_C$
<hr/>	
YP of F_1 Plants	$(A + C) \pm \sigma_A$

The number of tests of adequate precision that could be made with a given outlay would be about half as great for the gamete-selection series as for the plant-selection series. In view of the increased frequency of exceptional genotypes in the gamete selection series, the smaller sample would have a much higher probability of including exceptional Midland genotypes than the larger.

During the past season direct evidence on some of these points was secured in a yield test, conducted in collaboration with D. C. Anderson, at Malta Bend, Mo. The items tested included outcross tests (on L317/Hy) of the following:

- (1) 41 Midland plants
- (2) 37 Midland/WF9 plants
- (3) the line WF9, (entered for increased precision as 4 items)
- (4) 6 other elite lines (38-11, R136, 940, C.I.7, Kys, and K4)
- (5) 10 F_1 's of elite lines, included to check the additive inheritance of YP.

Groups (1) and (2) each included 27 plants representing a wholly unselected sample, with additional plants from visual selection which proved unrelated to yield. These two groups thus represent respectively the zygote and the gamete population of the Midland stock used. The test was planted as a 10 x 10 triple lattice, with 12 replications.

Calculation of the data is not yet completed but the results in general are evident from direct calculation as a randomized block experiment. On this basis the least significant difference is 4.5 bu. per acre. The test-cross yields of the Midland plants varied from 60.3 to 77.8. Those of the 7 elite lines ranged from 61.8 to 77.0, that of WF9 being 64.1 bu. per acre. The test-cross yields of the F_1 's and parent inbred lines were in general in good agreement with expectation on the additive basis, though the differences between the lines crossed are not large enough to make this a very significant test of YP inheritance. The test-cross yields of the Midland/WF9 plants indicated yield levels for homozygotes of the Midland gamete genotypes ranging from 46.8 to 83.8 bu. per acre.

Seed was produced in 1944 for a further trial of plant and gamete selection in the varieties, Kansas Sunflower, Clarage, and Midland, with certain modifications of method. It may be desirable in practice to apply gamete selection not to the unselected gamete population but to a selected population secured from the exceptional plants identified by a preliminary test-controlled plant selection. To test the feasibility of this modification, the unselected plants in the varieties mentioned are selfed and test-crossed as before and are also crossed on the inbred line selected for use in gamete selection. The gamete selection series from unselected plants may be made up from these crosses, and that from selected plants or mixtures may be made up from them after the plant selection tests have been made. Each variety thus yields three distribution curves, representing the unselected plant population, the unselected gamete population and the selected gamete population. Among the inbred lines included for comparison are K4, a line of excellent performance which was extracted from Kansas Sunflower, K201C, an excellent line extracted from Midland; and 3 Ohio lines which represent the best extractions previously made from Clarage. The position of these lines on the plant and gamete distribution curves of their parent varieties should provide a more definite basis for estimating the possibilities of plant and gamete selection as compared with the methods used in producing our present inbreds.

L. J. Stadler

2. Redox relationships in the development of anthocyanin. Keeble and Armstrong, Wheldale-Onslow, Atkins, and others have presented evidence suggesting the presence of oxidase enzymes and an oxidation system associated with the development of anthocyanin. In repeating the studies made by these early workers it is possible, in the light of revised redox methods, to correct several of the interpretations of the

use of oxidase indicators, and it now appears that the oxidase enzyme of the earlier workers is in fact a lipid absorptive and oxidative system. It became increasingly apparent during the course of the present study that there is a localized absorption of the oxidized form of the common redox indicators in unsaturated fats present in anthocyanin bearing cells. The oxidation of p-phenelenediamine, α -naphthol, leuco methylene blue and related indicators prior to their introduction into sections of rch and r \bar{g} tissue will give, in uniform and comparably cut sections, a greater localization of colored indicator in rch tissue. An iodimetric method applied to this absorptive system, in appropriately prepared tissue, has made possible a qualitative study of differences between colored (rch) and colorless (r \bar{g}) tissue and has given an exact iodine number for different tissues where weak anthocyanin development, dependent upon R alleles, is to be compared with more strongly colored rch tissue.

Iodine absorption is always greater in anthocyanin bearing cells; hence practicable microscopic qualitative observations may be compared with macroscopic anthocyanin distribution, and differences in intensity of pigmentation, by using the iodine number as a qualitative guide. The higher iodine absorption of anthocyanin bearing tissue may be seen to be localized in free plasmal lipids, in lipid material localized in "mitochondrial" or lipoclastic bodies in the cell, and in lipids impregnating cellulose walls. The lipids are highly unsaturated condensation aggregates and not true glycerides. They are not readily soluble in ordinary fat solvents but are soluble in petroleum ether after preliminary hydrolysis of the tissue and extraction with an alkaline/alcoholic mixture. The unsaturated lipids in colorless (r \bar{g}) tissue have a higher peroxide number as determined by oxidation of ferrous ammonium sulphate. The extracted lipids from rch tissue have 40% greater absorptive capacity (Wij's Iodine Method) than comparable extracts from r \bar{g} tissue. Presented in the table below are the iodine numbers of leaf tissue of rch and r \bar{g} sib comparisons, as determined by halogen solutions of increasing concentration. The samples were hydrolyzed to prevent iodine addition to starch and to facilitate iodine addition to unsaturated bonds; they were dried under nitrogen to constant weight and a standard iodine method with thiosulphate titration was used and endpoints were determined galvanometrically in some cases. The samples used ranged in weight from 0.020 mg. to 0.155 mg. so that the method may be applied to small samples of tissue that are held in ethyl alcohol (not above 50%), in order to remove chlorophyll, anthocyanin, etc., with frequent changes of alcohol to facilitate elution. At all stages in the process storage under nitrogen prevents oxidative degradation and a drop in iodine values.

Halogen solutions of increasing concentration

	I	II	III	IV
r ^{ch}	3.55	9.24	12.55	50.54
r ^{\bar{g}}	2.21	6.91	10.34	44.22

Using the methods outlined above a study was made of the development of pigment in excised leaves in culture. It was found that additions of dilute emulsions of unsaturated fats (corn oil, soybean oil, linseed oil) and various terpenes (thujone, etc.) greatly increased the production of pigment, but only when sugar was also present. Glucose solutions (16×10^{-3} molar) were less effective than glucose (8×10^{-3} molar) plus unsaturated fat emulsions (.4%). Holding the cultures under anaerobic conditions (under nitrogen) for the first two days of a culture study inhibits production of anthocyanin but increases overall pigmentation after aerobic conditions are restored. In the table below are the iodine numbers from a typical sugar culture experiment. A marked decline in iodine number in $r\bar{g}$ and a final rise in r^{ch} with pigmentation is clearly demonstrated.

All tissue from same leaf

	r^{ch}	$r\bar{g}$
Fresh Tissue	45.95 (colorless)	51.90 (colorless)
Sugar/Anaerobic	41.70 "	44.22 "
Sugar/Same as above, but exposed to air one day.	50.54 (Anthocyanin)	40.02 "

In vitro preparations of anthocyanin extracts and unsaturated fat emulsions reveal that anthocyanin is a hydrogen acceptor and acts to dehydrogenate and oxidize the fat, and the anthocyanin becomes partially reduced and in some cases irreversibly reduced. This dehydrogenation of fat emulsions by anthocyanin is stronger when water extracts of r^{ch} tissues are added to the emulsions. Microscopic sections of anthocyanin-bearing tissue held under anaerobic conditions and at a pH of 7.0 to 7.4 show a reduction (loss of color) of anthocyanin in lipid granules in the plasma under intense illumination and a restoration of color on diminishing the light. This is direct evidence of a reversible redox relationship between lipids and anthocyanin pigments.

It is generally true that anthocyanin bearing cells are epidermal, hypodermal or bundle sheath cells which have an excess of lipid material, and it is a general rule that cells low in lipids are lacking in anthocyanin. This fact may be determined by iodine staining in combination with extraction methods outlined above. It is illustrated in corn by the siliceous epidermal cell which, unlike its couplet partner, the fat-bearing suberized cell, lacks anthocyanin unless cultured in sugar/fat media under nitrogen followed by oxygen. Fatty and other organic acids, as revealed through the use of polychrome stains and direct acid value determinations are present in anthocyanin bearing cells before pigment is produced and there are apparently less free acids after pigment production.

Preliminary trials on B determined pigmentation indicate there is in lipid/pigment development a redox relationship similar to that obtaining in R^r alleles. Trials on the other higher plants

(Andropogon, Coleus, Petunia, Acer, etc.) reveal a similar redox problem in floral and autumnal anthocyanin development.

In summation, it now appears that the oxidase system, believed by early workers to be causal in anthocyanin development, is in reality a reflection of the oxidized and dehydrogenated state of lipids which absorb and possibly oxidize redox indicators. The absorption of iodine by these dehydrogenated lipids reveals qualitative but not absolute quantitative differences between pigmented and non-pigmented tissues. Anthocyanin acts in vitro to bring about the dehydrogenation of fats, and wherever anthocyanin appears in the plant associated with a lipid system the fats are more dehydrogenated than in comparable non-pigmented tissue.

D. S. Van Fleet

3. Comparison of ultraviolet and X-ray deficiencies. Earlier examinations of ultraviolet induced deficiencies in maize indicated that they were terminal, whereas X-ray deficiencies appeared to be usually, perhaps always, internal. Since non-homologous pairing of pachytene chromosomes frequently occurs, this point could be settled only by a study of a chromosome arm with a terminal cytological marker. In order to select plants with breaks in this arm, a gene affecting a seedling character was essential. Enoades reported bronze (bz) in the short arm of chromosome 9 (corn letter 1943). It was found that in the presence of certain R^F alleles, distinct color developed at the tip of seedling leaves with Bz but failed to develop with bz. Deficiencies of the bronze locus were induced by irradiation of mature pollen from a knob-bed-9 stock, wx-Bz-knob. Pollinations were made on a homozygous or heterozygous bz stock, Wx-bz. The colorless-tip F_1 plants which subsequently developed bronze pigment instead of anthocyanin furnished the cytological material. The usual acetocarmine smear technique was employed.

In the ultraviolet group, 3513 seedlings were examined of which 9 possibly tipless died in early seedling stage and 9 were bronze plants. In the X-ray group, 1670 seedlings were examined, of which 7 possibly tipless died in the early seedling stage and 11 were bronze plants. The cytological study of the bronze plants is summarized in the table.

Kinds of Chromosomal Change

No. bz plants	Haploid	1 break	2 break rearrangement			Not ana- lyzed
		Term. def.	Int. def.	Ring Chro- mosome	Def. : trans.	
Ultra- violet						
9	2	4	0	0	2	1
X-ray						
11	0	0	1	3	5	2

In the ultraviolet material single breaks in the short arm of chromosome 9 gave terminal deficiencies (with the loss of the knob) in 4 plants. The shortest deficiency, about one-third of the arm, removed the bronze locus and gave less than 1% crossing over between the break and the wx locus. In two cases breaks in different chromosomes were followed by rearrangement in such a way that parts of both chromosomes were lost and only one translocation chromosome survived. These have been called deficiency translocations. In pachytene the translocation chromosome pairs homologously with parts of the two normal chromosomes, and the two single strands usually pair non-homologously to give a three-armed translocation figure. At diakinesis and metaphase I, this association appears as a chain of three chromosomes or, less frequently, as a pair and a univalent. Anaphase I shows 9-10 separations or occasionally 9-9 with a lagging univalent. Pachytene preparations were not clear enough to determine exact points of breakage in the chromosomes.

All X-ray deficiencies resulted from rearrangements involving two breaks within the same cell. In one case both breaks were in the short arm of chromosome 9, giving an internal deficiency. In 3 cases breaks occurred in both arms of 9, a ring fragment which included the centromere being formed. Five deficiency translocations were found. In the case giving the best cytological preparations (involving chromosomes 9 and 5) both breaks appeared to be at or very near the spindle fiber regions. There were no cases of terminal deficiency.

Many plants with deficiency translocations (in this and other material) show a higher percentage of normal pollen than can be accounted for by random distribution of the three associated chromosomes at the first meiotic division.

Katherine O. De Boer

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R. L. Cushing
Cornell University

III. SEED STOCKS PROPAGATED IN 1944

Slightly more than 200 cultures were grown last summer. About half of these were the F_1 hybrids between weak stocks and non-related inbreds made by Dr. Murray in 1943. A few plants were selfed in each of these cultures. This program was carried along by growing still other weak stocks and crossing them with inbreds. It is hoped that in the course of a few years most of the useful genes can be put into vigorous combinations of this kind. In cooperation with Dr. Randolph, a beginning was made of the transfer of a good marker gene or two to each of the trisomic stocks now available. Combinations involving trisomic V, VI, IX, and X were obtained this year.

R. L. Cushing and Rosalind Morris

MAIZE GENETICS COOPERATION

NEWS LETTER

20

April 15, 1946

The data presented here are not to be used in
publications without the consent of the authors.

Department of Plant Breeding
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CORNELL UNIVERSITY
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 DEPARTMENT OF PLANT-BREEDING
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CORNELL UNIVERSITY
COLLEGE OF AGRICULTURE
DEPARTMENT OF PLANT-BREEDING
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2.

ANNOUNCEMENT

Arrangements have been made to continue the Maize Genetics Coöperation at Cornell University for a period of not less than three years. Professor R. L. Cushing, who has been responsible for the work done during the past few years, will help initiate Professor H. H. Smith who will have charge of the work in the immediate future. The undersigned will enjoy looking on from the outside and offering gratuitous advice as usual.

R. A. Emerson

I. REPORTS FROM COÖPERATORS

Connecticut Agricultural Experiment Station
New Haven, Connecticut

1. In the second generation from crosses of deviating lines with the original normal line, mono-factorial segregation is indicated by dwarf plant, pale top and crooked stalk. (Backcrossed ratio 52 tall; 32 dwarf where 42:42 were expected. F₂ selfed 49 green straight, 9 green crooked, 23 pale straight, 3 pale crooked where 47:15:15:5 were expected.) Narrow leaf cannot be separated clearly from normal in individual plants. F₃ progenies ranged in average leaf width from 74 to 93 mm compared to 72 for narrow and 92 for normal under similar conditions. Average height ranged from 92 to 103 inches compared with 91 for narrow and 95 for normal. In previous tests narrow leaf plants have been slightly taller than normal. Both the extracted homozygous normals and deviates have come out of the cross slightly enlarged, an indication that other factors are involved. Further testing is necessary to establish the significance of these differences.

Blotched leaf and late-flowering types have not yet been compared after extraction from the cross with normal.

In view of the fact that the long inbred Leaming lines continued to decline in yield during 20 generations it is quite possible that these lines which have not been selfed continuously for this length of time are still segregating for minor physiological changes along with the visible morphological changes which seem to be mutations.

The normal lines, in the two cases tested, show no increases when crossed with the same normal lines from which they have been separate for many generations. Therefore, the possibility of accumulation of dominant genes from both parents seems to be ruled out. Further testing of this point is needed.

There is the possibility of mutations or delayed segregations affecting combining ability that have no visible effect in the homozygous condition or in crosses with the same line from other sources. Three of the long inbred Leaming lines selfed for eight and nine generations were separated into two sub lines each and maintained separately for seven additional generations of self-fertilization. During this period they showed no visible differences but when intercrossed they all gave significant increases in some measurable character.

Two of these lines were again separated in the 17th and 22nd generations and further self-fertilized for eleven and six generations. When the first generation crosses between these sub lines were compared with their normal parents no significant differences were obtained. In one of these cases the parental lines

differed slightly in visible characters. All of this evidence indicates delayed segregation from an enforced heterozygous complex.

Five of the six deviating lines which show heterosis when crossed back to the normal line have been tested in outcrosses with unrelated lines. No significant differences in yield of grain were obtained between crosses of normal by unrelated normal compared to deviating line by the same unrelated normal. For practical purposes it is important that there were no decreases in yield.

D. F. Jones

2. A method for making smears of root tip chromosomes. Frequently it is necessary to have counts of root tip chromosomes, but the paraffin method for making preparations is laborious and time consuming. However, excellent figures can be obtained quickly and easily by the following technique. Fix young root tips in Carnoy's fluid for 6-24 hours. Change to 70% alcohol. (The material can be kept here until it is convenient to make the smears). Transfer to equal parts of hydrochloric acid and 95% alcohol for five minutes, then to 70% alcohol for at least five minutes. Put a thin cross-section slice of the root tip into a drop of aceto-carmin on a slide, and tease the material apart with needles, or flatten it with a scalpel. Put on a clean cover glass and press gently with the eraser end of a pencil. Heat slide several times by passing through a flame. Examine to see whether there are sufficient division figures. If not, make a smear from a different section of the root, or from a different root. A good preparation has the cells well separated but intact, with many well-stained division figures. Temporary mounts can be sealed with a gum-mastic-paraffin mixture and kept in a cool place for several weeks. Or the slides may be made permanent by McClintock's method for making sporocyte smears permanent.

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Ga₄ and pericarp-color ratios. In two earlier News Letters (17: 8-10, 1943 and 18: 7-8, 1944), aberrant pericarp-color ratios were reported and a gamete factor, Ga₄, was postulated as interfering with the functioning of pollen carrying it. There are now available more data like those previously reported and also a few of more nearly crucial importance. The records here assembled include both the new and most of the previously reported data.

The study involves crosses of lines having red pericarp and cob with lines having colorless pericarp and either white or red cob color. In this account, cob color will be disregarded, except in one section where its designation is essential. In general red and colorless (white) pericarp will be designated, respectively, by R and W. When reference to both pericarp and cob colors is made, the following symbols will be used for the three alleles:

R-R = red pericarp, red cob
 W-R = white pericarp, red cob
 W-W = white pericarp, white cob

Certain plants with heterozygous red pericarp, when selfed or used as pollen parents in crosses with white, give progenies with an excess of white-eared individuals, instead of the respective 3-1 and 1-1 ratios ordinarily observed. When, however, the same red eared plants are used as pistillate parents in crosses with white, normal ratios result. The ratios of red to white that have been observed to date in all aberrant cultures of whatever generations are given in the tabular statement below, together with first and later generations of crosses in which heterozygous reds were used as pistillate parents.

Parent plants Type	Number	Progenies		Ratio		% Red
		Number Red	plants White	R	W	
W/R (x)	49	1251	1085	1.15:1		53.6
W/(W/R)	25	491	1822	1:3.71		21.2
(W/R)/W	18	437	453	1:1.04		49.1

Not all red eared plants of cultures with an excess of whites, give aberrant ratios in the next generation. Of 42 plants tested from cultures resulting from W/(W/R), line 2 of the above table, 29 gave aberrant and 13 normal ratios in the following generations. Reds of aberrant cultures, which give normal ratios in later generations, are assumed to have lost Ga 4 by crossing over. But the relative numbers of aberrant and normal progenies resulting is not a measure of the percent of crossing over, because crossover pollen lacking Ga 4 is more likely to function in fertilization than pollen carrying Ga 4.

Of red eared F₂ plants lacking Ga 4, two out of three in general are expected to be homozygous. Of 61 such red eared plants of aberrant cultures, only 5 were homozygous, a ratio of 11.2:1 instead of the normal 2-1 ratio. Here again, this ratio is not a measure of percent of crossing over between red and Ga 4 alone or of percent of functioning Ga 4 pollen alone, for both variables are involved together.

Of red eared plants of normal cultures resulting from (W/R)/W, line 3 of the table above (like those of the reciprocal cross W/(W/R), line 2), some have normal and some aberrant progenies in the next

generation. Of 28 such reds tested, 23 gave aberrant and 5 normal ratios in the following generation. Since there is here no question of pollen differentials, the percent of normal cultures should measure the percent of crossing over in megasporogenesis. The percent of crossing over indicated is 17.9, but the number of plants tested is far too small to give reliable results.

Of the homozygous red eared plants occurring in aberrant cultures, one was crossed reciprocally with white and two others were used only as pollen parents in crosses with white. The progenies were all red eared, but, of course, segregated in the next generation. The ratios of red to white in the segregating generation indicated that the three homozygous red parents were heterozygous for Ga 4. The available data are summarized in the following table.

Type of cross	Number	Progenies	
		Red	White
W/ [(W/W)/(R/R)]	{ 7 8	292	901
		260	263
[(W/W)/(R/R)] (x)	{ 2 13	40	31
		729	263
[(R/R)/(W/W)] (x)	{ 5 6	98	69
		112	38

Of 30 segregating cultures from crosses involving homozygous red as pollen parents, 9 exhibited aberrant and 21 normal ratios. Of 11 segregating cultures from the one cross in which homozygous red was used as pistillate parent, 5 gave aberrant and 6 normal ratios. The second of these two categories (homozygous red as pistillate parent) should include equal numbers of aberrantly and normally segregating cultures, since, in homozygous red, crossing over with Ga 4 is not detectable and because Ga 4 was not present in the white pollen parent. The 5-6 ratio is as near equality as is possible with a total of eleven.

The first of the two categories (homozygous red as pollen parent) should, however, afford a direct measure of the percent of functioning Ga 4 pollen. Here crossing over in microsporogenesis cannot be detected and should have no effect on the ratio of aberrant to normal segregating cultures in the succeeding generation. Of the 30 F₁ plants tested, 9 gave aberrant and 21 normal segregation ratios. This 9-21 ratio indicates that 30 percent of the functioning pollen carried Ga 4, where 50 percent would be expected if this gene did not work to the disadvantage of the pollen carrying it.

When, in heterozygous red, the Ga 4 gene is lost from red-carrying gametes, it should be picked up in an equal number of instances by gametes carrying white. For this study, a third allele, colorless pericarp with red cob, W-R, may be used. When plants heterozygous for R-R and W-W are crossed with W-R, the red eared plants are W-R/R-R or R-R/W-R and the colorless eared plants are W-R/W-W or W-W/W-R. Data involving the first of these categories have been presented without reference to cob color. In the second category, pericarp is colorless throughout, but it is perhaps less confusing to designate both pericarp and cob color by symbols for the three alleles involved.

When, by crossing over, Ga 4 is shifted from association with R-R to the W-W allele, segregating progenies should show a deficiency of white. In the studies of crosses of R-R with W-W, out-crosses with W-R, as either pollen or pistillate parent, have afforded tests of 137 W-R plants. Their progenies, classified as having normal or aberrant segregation ratios of red to white cob, are summarized as follows.

		Number	Progenies		Ratio	%
			W-R	W-W	W-R:W-W	W-W
$\left[\begin{array}{c} \overline{W-W/W-R} \\ \text{and} \\ W-R/W-W \end{array} \right]$	(x)	$\left\{ \begin{array}{c} 117 \\ 20 \end{array} \right.$	2880 705	1016 44	2.83:1 16.02:1	26.1 5.9

In these cob-color studies, as in the pericarp-color work reported earlier in this account, when heterozygous red (R-R/W-W or W-W/R-R) is used as the pollen parent in crosses with W-R, there are involved both variables, namely, percent of functioning Ga 4 pollen and percent of crossing over. It is, therefore, impossible to evaluate either one of them. When, however, heterozygous red with heterozygous Ga 4 is used as the pistillate parent and homozygous W-R as the pollen parent, differential fertilization because of Ga 4 is eliminated, and the percent of crossing over in megasporogenesis should be indicated by the relative numbers of normally and aberrantly segregating cultures in the succeeding generation. Data are available for 32 such cultures, as follows.

Progenies of W-W/W-R						
Type	No.	Red	White	Ratio		%
				Red	White	White
$\left(\frac{W-W}{R-R} + \frac{Ga\ 4}{W-R} \right) (x)$	$\begin{Bmatrix} 28 \\ 4 \end{Bmatrix}$	693 114	232 5	2.99:1 22.8:1		25.1 4.2

Here the ratio of normal to aberrant progenies is 28:4, or 7:1. The percent of aberrant progenies — equivalent to percent of crossing over — is 12.5. It will be recalled that the study of segregating red pericarp, reported earlier in this account, involving 23 aberrant to 5 normal progenies, indicated a percent of crossing over of 17.9. The percent calculated from both the pericarp-color and the cob-color lots, 60 progenies in all, is 15.0. It will be recalled also that crosses of white with homozygous red pericarp, the latter as pollen parent, resulted in 21 normal and 9 aberrant cultures. This indicates that 30 percent of the functioning pollen carried Ga₄ and 70 percent carried its normal allele.

It remains now to see how nearly aberrant ratios correspond to ratios calculated from the indicated values of the two variables. The answer is easy. They do not fit at all well! It is realized that the number of progenies on which the evaluation of the two variables has been based is wholly inadequate — 60 for percent of crossing over and 30 for percent of functioning Ga₄ pollen.

One further method of evaluating the two variables is available. This method was used by Mangelsdorf and Jones (Genetics 11:423-455. 1926) in their study of the gamete factor in the fourth chromosome. By the use of data involving two genes both linked with Ga, they were able to evaluate the two variables simultaneously. This method can be used with data presented previously. (News Letter 17: 8-10. 1943). These are backcross data involving pericarp color and ms 17, with a total of 206 plants. The method of Mangelsdorf and Jones applied to these data indicates approximately 13 percent crossing over between Ga₄ and pericarp color — not far from that calculated by the method of eliminating one variable — but only 5 — instead of 30 — percent of the effective pollen carrying Ga₄. These percentages, when applied to the data summarized in this account, show a much better fit to observed ratios than do those obtained from evaluation of the two variables independently as presented earlier in this account. A comparison of the two methods is given in the following table.

		Ratios			
		Observed	Calculated		
			13	% cross- ing over	15
			5	% <u>Ga</u> 4 pollen	30
Coupling --					
B-C	-- Red to white	1 - 3.7	1 - 5.1	1 - 1.8	
F ₂	-- Red to white	1.2 - 1	1.4 - 1	2.1 - 1	
F ₂	-- Hetero- to homo- zygous red	11.2 - 1	6.2 - 1	2.8 - 1	
Repulsion					
F ₂	-- Red to white	16.0 - 1	11.3 - 1	3.6 - 1	

The data presented in the 1943 News Letter indicate that Ga₄ is to the left of ms17. On the assumption of 13 percent crossing over between P and Ga₄, the map may be given tentatively as below.

sr ←----- Ga₄ ←----- 10 -----→ ms17 ←----- 3 -----→ P ----- br

A further study, involving Ga₄ with sr, ms17, P, and zb₄, is underway, but little further evidence can be obtained short of two more years.

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Regression Analyses of Yields of Hybrid Corn and Inbred Parent Lines.-- 1. Derivation of a theoretical regression function. For n loci let the basic effect of a gene substitution be d , dominance effect kd , proportions of loci AA in P_1 and P_2 be u and w , the multiple recessive phenotype T , and gene action additive.

$$\begin{aligned} P_1 &= 2und + T, & P_2 &= 2wd + T, \\ F_1 &= 2uwnd + [u(1-w) + w(1-u)](nd + nkd) + T, \\ F_1 &= (1 + k + kT/nd) (P_1 + P_2)/2 - (k/2nd)P_1P_2 - (k/2nd)T^2 - kT, \\ F_1 &= b_1 P - b_2 P_1P_2 + C_1, \text{ where } P = (P_1 + P_2)/2 \end{aligned}$$

With each generation of selfing $1/2$ of dominance effects disappear. Divide each term in k by 2 for each time selfed to obtain the general function for F_n . This function is a surface which is curved if there is any dominance (k not zero). (Regression of F_1 on mean of parents neglects the second term of the function. A plane is fitted where a curved surface provides a closer fit if there is dominance).

Regression of F_1 on P_2 with constant P_1 (any single F_1 column in Stringfield's table below) is obtained by treating P_1 as a constant in the main function.

$$F_1 = [1/2 + k/2 - k(P_1 - T)/2nd] P_2 + C_2$$

The partial regression coefficient b_p is contained in the brackets. Its value manifestly depends upon the value of constant P_1 . P_2 is the independent variable. Substitution of AA for aa at one locus in P_2 provides an increment $2d$. The corresponding increment of F_1 is $[1/2 + k/2 - k(P_1 - T)/2nd] 2d$. The first term of this expression, $(1/2)2d = d$, accounts for the basic effect of an additional A allele in F_1 coming from P_2 . The second term, $(k/2)2d = kd$, provides a dominance effect. If, however, P_1 is AA at that locus no dominance effect will be added to F_1 by the substitution, and the one already there will disappear. P_1 is AA at u loci, and $(P_1 - T)/2nd = u$. The third term adds $[-k(P_1 - T)/2nd] 2d = -2ukd$.

Under the assumptions, our main function calculates exactly mean F_1 for any type pair of parent values. Variance from such means, or deviations from the regression surface are due solely to variations in degree of heterozygosity. This portion of the variance is beyond parent criteria. Present parent criteria P and P_1P_2 together provide maximum estimation of F_1 by parent criteria. It is clear that the mean degree of heterozygosity is greater in crosses of good x poor lines than in crosses of medium x medium lines and that the product of parents P_1P_2 is included to measure that variation. It must also be clear that the various genetic interpretations inserted along have not been employed in the mathematical derivations. For the most part they were not recognized until after completion of the algebraic formulations.

Finally regression of bp on P_1 is given by the formula for bp. The regression coefficient is $(-k/2nd)$ which is b_2 of the main function. It will be labeled b_2 here also since the two coefficients are identical.

2. Fitting the functions to data. An unpublished table kindly furnished by Mr. G. H. Stringfield is included to illustrate the process of fitting. Values of bp at the bottom are simply regressions of F_1 of the respective columns on P_2 . Regression of the values of bp at the bottom of the table on the values of P_1 at the top is -0.015 , and the correlation is -0.98 which is highly significant.

F_1 and parents, bushels per acre, (G. H. Stringfield, unpublished)

P_1	::	:	:	:	:	:	:
	::	4-8 :	90 :	Hy :	02 :	WF9 :	51 :
P_2	::	13.6 :	28.2 :	29.8 :	46.1 :	51.4 :	55.3 :
<hr/>							
4-8, 13.6	::	:	76.7 :	96.3 :	91.0 :	100.7 :	106.1 :
	::	:	:	:	:	:	:
90, 28.2	::	76.7 :	:	81.4 :	94.2 :	97.9 :	86.4 :
	::	:	:	:	:	:	:
Hy, 29.8	::	96.3 :	81.4 :	:	108.9 :	109.8 :	94.7 :
	::	:	:	:	:	:	:
02, 46.1	::	91.0 :	94.2 :	108.9 :	:	104.0 :	100.8 :
	::	:	:	:	:	:	:
WF9 51.4	::	100.7 :	97.9 :	109.8 :	104.0 :	:	103.4 :
	::	:	:	:	:	:	:
51, 55.3	::	106.1 :	86.4 :	94.7 :	100.8 :	103.4 :	:
	::	:	:	:	:	:	:
<hr/>							
bp	::	.68 :	.408 :	:	:	.048 :	:
	::	.6947 :	.4060 :	.3433 :	.2314 :	.0516 :	.0512 :
<hr/>							
Mean P_2	::	42.0 :	39.2 :	38.8 :	35.6 :	34.6 :	33.8 :
<hr/>							
Mean F_1	::	94.2 :	87.2 :	98.2 :	99.8 :	103.2 :	98.2 :

From this regression the estimated value of P_1 for $bp = 0$ is 57.1 bushels per acre which is just beyond the range of the data. The same process has been applied to the other sets of data listed in the second table. Where significant values of b_2 have been obtained the main multiple regression function has also been fitted. In each case the second estimate of b_2 agreed closely with the first one, which provides a computation check since the two are algebraically identical also in the computation formulas.

The last five items in the table were then computed by quadratic solution of the multiple regression function on the assumption that where P_1 and P_2 are both completely aa or completely AA, $P_1 = P_2 = F_1 = F_2$. Roots thus obtained are estimates of the bottom recessive and top dominant.

3. Interpretation. First I must note that I have never had any notion that yield of corn could depend upon a multiple set of genes with uniform d and kd from locus to locus. Variation of d and of kd must contribute to the variance of F_1 and thus provide additional variance from the present regression surface. Beyond that I doubt that variation of d and kd could confuse present analyses.

Evidence here for overdominance (no dominance, $k = 0$; complete dominance $k = \pm 1$; overdominance k numerically greater than one) seems to lie in the estimated values of P_1 for zero partial regression. If dominance is complete, zero partial regression will obtain only when P_1 is the top dominant. This statement agrees with long held genetic philosophy of prepotence. That it is mathematically true in present theory may be seen by setting $bp = 0$ and $k = 1$ in the partial regression coefficient formula and solving to find $(P_1 - T)/2nd = u = 1$. Note also that with complete dominance the top dominant and top heterozygote are equal. Since for present data, values of completely prepotent P_1 , ($bp = 0$), are far below mean F_1 , the only direct interpretation is overdominance, see values of k estimated from the data. It would seem to make no difference whether the genes of P_1 and P_2 are completely linked or completely independent, so far as immediate contributions to F_1 are concerned.

Fisher, (Genetical Theory of Natural Selection) gives the condition for equilibrium where the heterozygote has selective advantage over both homozygotes for one pair. His mathematical condition is identical with the present one for $bp = 0$ for any value of k (Selective advantage) except that his condition is in terms of the proportions of a and A alleles in the population at equilibrium. The present condition is in terms of u , the proportion of loci AA in P_1 . If many loci are all at Fisher equilibrium in a cross breeding variety the expected value of u for a homozygote derived without bias is identical with \bar{q} for the variety. Or if \bar{u} for a group of lines is identical with \bar{q} for equilibrium the lines as a set are at equilibrium. Every line, good or poor, will then have the same general combining ability as measured by the average of its crosses with all of the other lines. Equilibrium for each locus is at the instant where a and A alleles combine equally well with the field.

REGRESSION ANALYSES OF YIELDS OF HYBRID CORN AND INBRED PARENT LINES

	Mean	Estimated: Mean F ₁ : Bottom	Top	Maximum	Maximum	
	partial	P for	recess-: domin-: F ₁ of	open-pollin-:		
	regress-:	bp = 0	ant	homozyg-: ating		k
	ion	b ₂	(T)	ous	variety	
				parents		
Stringfield, ¹ F ₁	0.30	-0.015**	96.8	88.5	146.3	1.87
F ₂	0.34	-0.009**	69.9	82.7	159.1	2.16
Kinman & Sprague, ² F ₁	0.42	-0.015*	79.9	76.2	120.0	1.64
F ₂	0.42	+0.005	50.8	-	-	-
Jorgensen & Brewbaker ³	0.04	-0.002	372.5	-	-	-
Nilsson-Leissner ⁴						
Dent I	0.28	-0.008**	314.5	224.1	369.9	2.08
Dent II	0.22	-0.004	130.5	-	-	-
Flint I	0.36	-0.0002	2430.2	-	-	-
Flint II	0.62	-0.0008	888.3	-	-	-
Jenkins, ⁵						
white '26	0.65	+0.018	-	-	-	-
early yellow, '26	0.38	-0.052**	-	-	-	-
later yellow, '26	0.10	+0.037	-	-	-	-
white, '27	-0.09	+0.153	-	-	-	-
yellow, '27	0.07	-0.002	-	-	-	-

1. Unpublished, see text.
 2. Jour. Am. Soc. Agron., May, 1945
 3. " " " Sept., 1927
 4. " " " May, 1927
 5. Jour. Agr. Res. Nov. 1, 1929

* Significant

** Highly significant

Jenkins (1929) almost attained that condition (last 3 entries in present table). For those data the partial regressions are nearly as frequently negative as positive and almost uniformly small numerically. After much selection Stringfield, and Kinman and Sprague studied groups of lines which show recession from the equilibrium which well selected varieties had closely approached 20 years or more ago. Recession may be due to mixing lines from different sources in one group and probably to selection for specific combining ability (more than average heterozygosity). The ceiling for hybrids is higher if one line has fewer AA loci, but this point can hardly be fully demonstrated without a 3-dimensional figure.

From the 3-dimensional figure for overdominance of the degree indicated ($k = 2$) it is clear that the F_1 trend for increasing P_1 and P_2 rises steeply over most of the range of present corn breeding experience which just laps over the crest. Beyond the trend is downwards. Beyond we have hardly gone, partly because of linkage as visioned by Jones and partly because present practice requires slight recession from the crest to another equilibrium between selection for specific combining ability and selection for general combining ability and excellence of lines themselves.

Present interpretations must remain in some degree tentative until lines well beyond the crest to provide significant negative partial regressions have been obtained. Before such evidence any alternative interpretation of complex, non-additive gene action would stand entirely refuted, I think. Excess of any heterozygote over the top dominant would seem to be overdominance by definition. The possibility of explaining present results by non-additive action without overdominance is very small insofar as I can tell but space does not permit more to be said here. Neither does space permit listing of every point where overdominance theory agrees with corn breeding experience more closely than does dominance theory. I have found no discrepancies and so must say that the evidence for overdominance must seem overwhelming but not crucial to any unprejudiced mind. It will be appreciated if any discrepancies are pointed out.

The same analysis has been employed with data on other characters of Jenkins (loc. cit.) with no evidence of overdominance and in most cases slight evidence of any dominance at all. Height of plant is an exception, but it depends largely on vigor. No data on ear dimensions have been available.

Fred H. Hull

1. Pod Corn. We now have fertile, true-breeding inbred lines of pod corn. These were obtained by selecting for minus modifiers of the tunicate condition. In these stocks the glumes show about the same development in the homozygous condition as is usually found in other stocks in the heterozygous condition. Seed of these inbred tunicate lines is now available in considerable quantity.

Varieties and inbred strains of maize differ greatly in their modifier complexes with respect to the tunicate character. When varieties and inbreds are crossed to the same stock of tunicate there is in the F_1 , considerable variation in the development of the glumes. Paraguayan and Bolivian varieties have strong minus modifier complexes. Guatemalan varieties have plus modifiers or at least are lacking in minus modifiers. North American inbred strains cover the entire range. Iowa 701 has a strong plus modifier complex while Minn. Al58 is so strongly minus that in some crosses with pod corn the tunicate ears are scarcely distinguishable from non-tunicate.

2. Modifiers of Secondary Pistillate Florets. The occurrence of varieties of maize in Bolivia in which there is a partial or complete development of the secondary pistillate floret, as in Country Gentleman sweet corn, suggests that this may be a primitive character. If this is the case, then there may well be differences in maize varieties in their modifier complexes with respect to this character. Preliminary studies made by crossing with an inbred strain of Country Gentleman indicate that Guatemalan varieties have strongly minus modifier complexes with respect to the development of secondary pistillate florets while Bolivian varieties have plus modifiers or are neutral. The results so far as they go, can be interpreted in terms of *Tripsacum* contamination in Guatemalan varieties and its absence in Bolivian varieties.

3. Nature of the Maize Ear. The hybrids of pod corn and Guarany maize, previously reported, which have been useful in demonstrating the nature of the ear of maize, have produced an additional useful abnormality. In 1945 several plants were found in which one or more ears were normal while other ears on the same stalks produced greatly elongated shanks. When this occurs the ear is more or less naked and the shucks which usually surround the ear become normal leaves spaced at intervals on an elongated lateral stem. There is no doubt that the ear was originally the terminal inflorescence of a lateral branch.

4. Derivatives of maize-teosinte crosses. The segments of chromatin or blocks of genes which distinguish various types of teosinte from maize have been transferred individually by repeated backcrossing to a uniform inbred strain of maize. Stocks derived by this procedure show that the segment which occurs on chromosome No. 4 in Florida teosinte has almost identical counterparts in Durango, Nobogame and "New" teosintes. Whether these counterparts occur on chromosome 4 in each of these teosintes remains to be determined.

These stocks are also useful for testing the effect of teosinte germplasm upon the yield of maize. Preliminary tests indicate that a small amount of teosinte germplasm may improve grain yield. When two or more segments are present, however, even in the heterozygous condition, grain yields are definitely depressed although forage yields may be somewhat improved.

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1. Sterility Studies:-- T1-5-6-7. Mr. Constancio Lazaro has continued his study of this stock in Uruguay. He has identified the chromosomes involved in a series of semisterile plants derived from the cross: (.)8 x Normal. Of these, 16 are T1-5 translocations, 6 are 1+5 or 7 (not 6) while only one is T6+(?). In addition to the derived semisterile lines, another derived type with about 65% pollen abortion and a ring of 6 chromosomes attached to the nucleolus was found here at Minnesota. Intercrosses are growing in the greenhouse to determine which chromosome pair has been lost from the ring of 8 chromosomes. Linkage tests with the (.)8 showed the following percentages of recombination: f - 22%; bm2 - 50%; y - 16%; v5 - 9%; bm - 8%; gl - 5%; ra - 3%. Recombination values and gene order in one T (1) ? -5 stock derived from the (.)8 are: bm 30 Pr 8.7 T; ys-T - 2%.

2. Yellow Endosperm.--One selfed ear had 112 deep yellow : 71 pale yellow : 14 white grains, a 9:6:1 ratio which may be interpreted as the interaction of two factors for pale yellow. Tassel-seed-4 was also segregating. The ratios for ts4 in the three classes suggest linkage of ts4 with one of the two pale yellow factors.

It should be possible eventually to identify stocks for the different yellow factors by their linkage with other characters, e.g. ms1 for Y, al for one chromosome 2, vp for another, etc.

3. Chromosome 6 Linkage Studies.--A stock of ms pb has been established. The linkage of pb with Y is very close.

Classification for su2 has not been very satisfactory in material grown here at Minnesota. The data reported by me in the Coop Letter of March 23, 1937 (p. 15) indicated the order y-pl-su2, with about 8% recombination between su2 and Pl. It was noted there that the separation for Yy was poor. Since then Horovitz et al. (Anales Inst. Fitotecn. S. Catalina 3:37, 1941) reported a su_x between Y and Pl. One backcross test with Pl using su2 as the female parent indicated 15% recombination, but all the recombinations were found in the non-sugary class. One test of su2 vs ms was set up as follows:
$$\begin{array}{c} (\underline{ms} +) \\ (+ \underline{su}_2) \end{array}$$

was crossed on a ms Su₂ Su₂ stock and the progeny grown. The open pollinated ears were examined to determine the number of homozygous Su₂ and heterozygous su₂ in the normal and ms classes, from which the per cent recombination can be calculated. The method seems to be usable. In this case, 32.8% recombination was observed between ms and su₂. These results are not satisfactory, however, since in the ms class there was 21.5% while in the non-ms class there was 45.4%. Intercrosses of su₂ with Horovitz's su_x have not been entirely satisfactory but they seem to indicate the two are the same.

Red glume collar in the tassel florets appears to show linkage with Pl in certain cultures, not in others.

A silky character is closely associated with antherless in the stock obtained from the Corn Coop. This silky vs Y showed 16.5% of recombination.

Trisomic tests for location of new factors in chromosome 6 : ba_s (barren stalk in a sweet corn), a new silky from a single cross, and a new stock of tinged (tn) show normal disomic ratios. The midget dwarf (mi) shows closer fit to a trisomic ratio than to disomic, although classification was not too certain.

C. R. Burnham

The following have assisted in the work at various periods: Gertrud Stanton, C. H. Li, T. J. Liang, and H. H. Highkin.

4. Miscellaneous Linkage Tests.-- For the new silky mentioned above, data from a small population suggest a linkage with pr. There is no close linkage indicated between narrow leaf-2 and: floury, yellow endosperm, colorless aleurone.

Linkage was reported previously between pr and sh₂ - sh₂ is closely linked with ag, no crossovers being found in an F₂ repulsion population of 1189.

There was a suggestion of linkage between yellow vs. pale yellow and the tinged mentioned above.

H. H. Highkin and C. R. Burnham

5. An "Oenothera" or Multiple Translocation Method of Establishing Homozygous Lines.-- A method by which a gametic combination could be made homozygous immediately should be of practical use to the plant breeder. One method, the utilization of haploids by doubling their chromosome number, has been suggested by many workers. It seems to be a feasible method in crops in which pollinations can be made on a large scale and genetic markers are available to aid in their recognition.

A second method for obtaining such homozygous lines is one I am calling an "Oenothera" or multiple translocation method. In this method, all the chromosomes of the haploid set are to be involved in translocations in such a way that the F₁ of crosses with normal stocks will have at meiosis a ring containing the entire diploid number of chromosomes. Such a plant should produce two kinds of functional spores corresponding to the two parental gametic combinations of chromosomes. Among the offspring from selfing such a plant there would be the heterozygotes with the chromosome ring recognizable by high spore abortion; and in addition two types of normals, each homozygous for one of the two parental gametic combinations. These two types of normals would have normal pollen, the normal number of chromosome pairs, and could be distinguished by crossing them with standard normal stocks.

The normal type not carrying the translocations would constitute the homozygous line.

The degree of homozygosity in these lines thus isolated depends on the amount of crossing over which has occurred at meiosis in the formation of the functional spores. Crossovers in the differential segments result for the most part in spores carrying interchanges and would be eliminated. Crossovers in the outer or interchanged arms of the chromosomes would be the ones most likely to result in recombinations of characters between the two parental gametes. The amount of recombination may not be very large, since crossing over is usually greatly reduced in regions near the translocation points and reduced to a lesser degree in regions farther away. It might be necessary, however, to establish several normal sub-lines from each F_1 plant to eliminate, or at least to measure, heterozygosity from that source.

For practical use, the multiple translocation stock would be crossed with the heterozygous source being used for new gene combinations (e.g. a variety, or a single- or double-cross hybrid). Each F_1 plant then represents a different gametic combination from that source combined with the multiple translocation gamete, and is the starting point of a different homozygous line to be established in F_2 . Selected lines thus isolated could be utilized in breeding tests similar to those used with lines heretofore established by continued inbreeding. The frequency of "superior" lines should correspond to the frequency of "superior" gametes in the heterozygous population being sampled. In this "Oenothera" method the gametic combination is established in homozygous condition immediately. In Stadler's "gamete selection" method, the selected gametic combination is combined with a gamete from an inbred line. Further breeding, selection and testing are necessary to isolate lines which carry at least part of the new germ plasm.

The "Oenothera" method has not been tried but crosses are under way by which it is hoped to eventually produce such a multiple translocation stock in corn. The plan of procedure is to choose for crossing only those translocations involving one chromosome in common in which the breaks in this common chromosome are far enough apart to furnish a "differential segment." A crossover in this segment will combine the two translocations in the same gamete.

Spore abortion will undoubtedly increase as more translocations are added, but it is hoped that it will not preclude dehiscence of the anthers or the production of sufficient seeds to utilize the method. It is possible that in the larger rings more of the disjunctions will fall into the zigzag type and thus reduce the degree of spore abortion.

C. R. Burnham

5. Notes on the Use of Maximum Likelihood Formulae for the Calculation of a Single Recombination Value for Data From Several Sources.-- (As applied by Immer and Henderson, Genetics 28:419-440, 1943.) Two methods are available, one being to weight each value according to its standard error. The other method is to combine the separate maximum likelihood formulae for each source into one formula, place it equal to zero, and solve for a value of p which best satisfies this equation. In using the second method as outlined, difficulties were encountered which were finally solved with Immer's help. Two changes must be made in the method as outlined.

1. The separate maximum likelihood formulae must not be reduced by any factor common to that portion (since it is not common to the other formulae being added to make up the one combined formula).
2. The maximum likelihood formulae as set up apply to repulsion. When used for coupling, the entire formula for that portion must be multiplied by (-1) (as shown by redifferentiating the basic equations).

The maximum likelihood formulae for the various sources of data become for F_2 consisting of (3:1) (3:1):

1. for F_2 repulsion:

$$2p \left(\frac{a}{2+p^2} - \frac{b+c}{1-p^2} + \frac{d}{p^2} \right) = 0$$

For F_2 coupling this is multiplied by (-1) . It must also be remembered in substituting that in coupling p is the non-recombination fraction or $(1 - \text{the recombination fraction})$.

2. For "singly dominant" F_2 plants classified into their genotypes in F_3 , the formula for repulsion is:

$$\frac{k}{p} - \frac{2j+k}{1-p} + \frac{(j+k)2p}{1-p^2} = 0, \text{ the same as given in the paper.}$$

For coupling the entire formula is multiplied by (-1) .

3. For "doubly dominant" F_2 plants classified into the relative numbers of heterozygous and homozygous genotypes, the formula for repulsion is:

$$\frac{2e+f+g}{p} - \frac{f+g}{1-p} - \frac{2(h+i)(1-2p)}{1-2p+2p^2} - \frac{(e+f+g+h+i)2p}{2+p^2} = 0$$

This is also the same as given in the paper.

For coupling the entire formula is multiplied by (-1) .

If linkage data from these three sources are available, these formulae are combined by addition into one maximum likelihood formula, the observed values substituted and the value of p which best satisfies this equation is determined.

The standard error to be applied to this value is calculated from the total amount of information furnished by the available data, since $S.E.p = \sqrt{\frac{1}{I_p}}$ where I_p is the total amount of information. I_p can be calculated easily by the method in Mather "Measurement of Linkage in Heredity", page 68.

A supplementary note to the paper in Genetics had been proposed by Immer.

H. H. Kramer and C. R. Burnham

Missouri Botanical Garden, St. Louis, Mo. and
Pioneer Hi-Bred Corn Company, Johnston, Iowa

Variations in Kernel Shape and Texture in Corn-Belt Maize.-- Typical kernels were selected from 140 different inbred lines of dent corn. These included as many of the standard inbreds such as 38-11, WF-9, etc. as could be obtained, together with some of the newer inbreds and various "second-cycle improvements" on older inbreds. Care was taken to obtain healthy and well-grown ears in spite of the weakness of some of the inbreds. As representative a kernel as possible was selected from each ear and the variation of the entire collection was repeatedly examined and compared with collections of open-pollinated varieties from various parts of the New World.

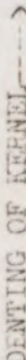
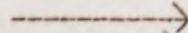
Much of the variation in this material, more than at first seemed possible, is accounted for by differences in the texture (hard dent, soft dent, etc.) and in the position at which the kernel shows its maximum width. The latter character varies from wedge-shaped kernels like WF-9 to broad-based, pointed ones like K 43. If a small percentage of "buckshot" and poorly developed kernels are excluded as too difficult to classify, the remainder show a clear set of transitional stages between these two extremes. At the one end is the flat, wedge-shaped kernel fairly similar to many of the older open-pollinated varieties. It is widest at its apex, and allowing for the shrinkage when it dents, it is also thicker at that point. Consequently it not only tapers to the base, it also slopes to the base (i.e. the narrowing is in two dimensions). The kernels at the other extreme are both wide and high at the base, bulging out broadly below and tapering conewise toward the apex.

Between these two extremes it is possible to select a whole series of intermediates. Those about in the middle are flattish kernels, widest in the middle and also slightly thicker there. It is

they and the ones even less pointed which are of most interest in this classification. It does not seem probable that one would have recognized what is apparently a slight degree of pointing, until he had seen all the intermediate types laid out in this way. These different kernel shapes seem to result from various intermediates between two fundamentally different growth patterns, similar to some of those which have been analyzed in Cucurbits by Sinnott.

The kernels were then classified for texture. At the one extreme (grade 1) were a few inbreds which showed no capping of soft starch. In the next class were those which were capped but not perceptibly dented. Next (grade 3) were both capped and dented but without a wrinkled pericarp due to the collapse of the soft starch area. Finally there was a class whose kernels were capped, dented, and with the pericarp distinctly wrinkled at the apex.

When these grades of denting and pointing had been determined, the entire collection was sorted out simultaneously for both characters. A few of the small kernels remained difficult to classify and there may well be other factors such as long kernels *vs.* wide kernels which need to be considered. However this simple two-way scheme worked surprisingly well and brought similar types together. The distribution was as follows:

DENTING OF KERNEL 	POINTING OF KERNEL 		
	Widest at apex	Widest at middle	Widest at base
GRADE 4	20	0	0
GRADE 3	26	26	12
GRADE 2	14	21	0
GRADE 1	7	11	3

Figures show No. of kernels in each class.

It will be seen that there is a fairly strong negative correlation between denting and pointing. The heavily dented kernels are all widest at the apex and the less the degree of denting the higher is the proportion of pointed kernels.

After the kernels had been laid out in this way it was apparent that certain other characters were correlated with pointing or with denting. The association of red pericarp with pointed kernels was particularly conspicuous. Of those widest at the apex only 7 percent were so affected whereas 10 percent of the medium pointed, and 53 percent of those widest at the base. This may be related to the fact that in Mexico, the supposed ancestral home of our dent corns, pointing of the kernels is very closely associated with red pericarp. Red pericarp was found to have no obvious connection with denting but blistering of the pericarp was strongly associated with denting, as well as negatively with pointing. Another feature which (though it varies greatly in its expression) is characteristic of

certain inbreds, is a silvery appearance of the pericarp, apparently due to air. This showed no association with denting but was strongly correlated with pointing.

After the above analysis had been made it was interesting to examine various inbred, single-cross, and open-pollinated varieties. The interaction of various factors in producing different types of dent corn is much clearer after such an examination. The production of a smooth, dimpled dent (such as characterizes OS 420 among the inbreds) is very evidently the combination of a high degree of denting with a fairly high degree of pointing. It is the pointing which shapes up the kernel and gives the ear its neat appearance.

Edgar Anderson (Missouri Botanical Garden)

Ray E. Snyder (Pioneer Hi-bred corn
Breeding Company)

New York State Agricultural Experiment Station
Geneva, New York

In the early summer of 1944 Professor S. Horovitz, of the Phytotechnical Institute of Santa Catalina, of Argentina, sent me some seeds of his new sugary (su_x). He and coworkers reported this new sugary in the *Anales del Instituto Fitotecnico de Santa Catalina* (1941) 3:37-44. He says there that it is on chromosome 6, and that it interacts with su_1 to make su_1 dominant.

The su_x was crossed with su_1 (the inbred, P51) as soon as possible; the F_1 seeds were starchy. Last summer I grew the F_1 and selfed four plants. Five classes of seeds appeared: starchy; su_x , which is waxy looking but stains black with I_2KI ; a smooth-sugary seed which is dented and translucent, but not wrinkled; ordinary sugary; and super-sugary (Horovitz's name), which is more wrinkled than ordinary sugary. Not only was there an extra class, but two of the four ears fit an extraordinary ratio, as shown below:

	87 (14) (x)			87 (3) (x)		
	87B (2) (x)			87B (5) (x)		
	Obs.	Ratio	Calc.	Obs.	Ratio	Calc.
Starchy	224	8	230.0	312	9	299.5
Sugary - x	61	2	57.5	56	2	66.6
Smooth sugary	35	1	28.8	35	1	33.3
Sugary - 1	83	3	86.3	93	3	100.0
Supersugary	57	2	57.5	37	1	33.3
	$x^2 = 1.84$			$x^2 = 3.20$		

If the four ears are assumed to be the same and are lumped together, the total counts do not fit either ratio, but are nearer to $8-1/2:2:1:3:1-1/2$. The classification of the various kinds of kernels is clear except between sugary and supersugary.

John Shafer, Jr.

Pioneer Hi-Bred Corn Company, Pioneer Laboratory,
Johnson, Iowa

The determination of chromosome knob numbers in the more important inbred lines of Corn Belt maize was started in the summer of 1945, of which a preliminary account may be made at this time. To date, approximately thirty inbred lines of dent corn, twelve open pollinated or inbred strains of popcorn, and five North American flints have been examined. Although these numbers are relatively small when compared with the total amount of material available, the results obtained reveal some rather interesting facts. Among the thirty dent corn inbreds studied, knob numbers are found to range from two to nine with a frequency distribution as indicated in figure (1). Knob numbers appear to be correlated with certain morphological characters of the ear. For example, those lines possessing high knob numbers have, in general, a more compressed base, more tapered ears, and higher numbers of rows of kernels than those with low numbers. There is also some evidence indicating that irregular rowing is associated with high knob number. Among the popcorn strains examined, all were found to possess median knob numbers (4-6). The most interesting observation encountered occurred in the 8-10 rowed North American flints which were found to be knobless or nearly so. Of the five lines examined, four were knobless and one contained a single knob. These data, it will be noted, are not entirely in agreement with what one would expect on the basis of the tripsacum hypothesis.

William L. Brown

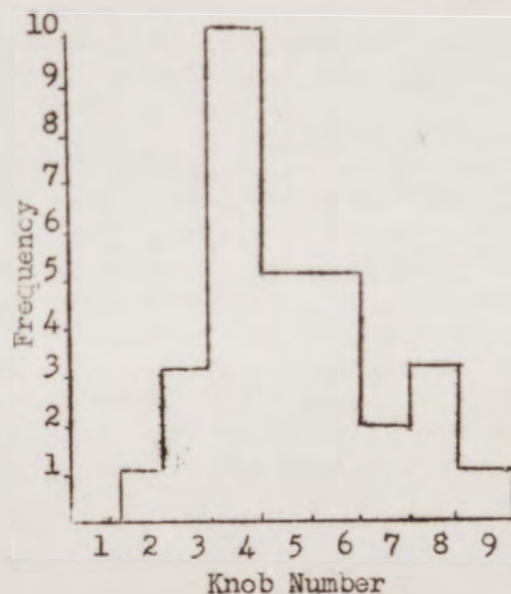


Fig. 1

University of S. Paulo,
"Luz de Queiroz" School of Agriculture, S. Paulo, Brazil

CORNELL UNIVERSITY 23.
COLLEGE OF AGRICULTURE
DEPARTMENT OF PLANT-BREEDING
ITHACA, N. Y.

1. The al gene is very closely linked to lg1 according to the following data obtained in F₂ (repulsion):

Pedigree NO.	++	+ <u>lg1</u>	al +	al <u>lg1</u>
754- 1	108	67	46	0
- 4	151	58	85	1
- 5	103	42	45	0
- 6	131	62	54	1
- 7	196	88	106	0
- 8	114	57	39	0
- 9	180	80	87	0
-11	118	46	56	1
-18	132	63	47	1
TOTAL	1233	563	565	4

Crosses involving al, lg1 and gl2 were made this summer (1945-October) in order to get the position of al in relation to lg1 and gl2 in chromosome 2.

2. One ear segregating for y3 showed female elimination for this condition. The cross made was Y1Y1Y3Y3Y5Y5 x Y1Y1Y3Y3Y5Y5 and the expected ratio 1 orange (Y1Y1Y3Y3) : 3 white (Y1Y1Y3Y3, Y1Y1Y3Y3, Y1Y1Y3Y3) was changed to 1 orange : 1 white (81 orange seeds : 66 white seeds). The orange seeds sowed were selfed and gave in all cases ears segregating for 9 orange : 7 white. The white seeds gave normal plants which when selfed produced ears segregating for albescent seedlings.

3. Material received from Dr. A. M. Brunson was sowed and is now being crossed with several Y-testers. The white seeds always gave albino plants and the dual effect of this mutation (provisionally called Yx) seems to me in favor of the hypothesis y3 that is identical with al.

4. Seeds received from Dr. Merle T. Jenkins were sowed and only the "dark yellow" germinated. The "lemon yellow" is very similar to some Y1 stocks I have and in my opinion must be called only "yellow" in order not to confuse it with the "lemon yellow" due to the yellow aleurone color. Dr. Jenkins' ratio 3 dark yellow (orange) : 1 yellow is identical with that I obtained in Brazilian strains (Maize News Letter 17:1943 and Amer. Nat. 79:187-192, 1945) and the gene producing the difference orange : yellow I called provisionally YD. Several crosses are now being made in order to try the location of YD and to see its interrelations with Dr. Jenkins' gene in chromosome 7.

5. My working hypothesis on the yellow-orange endosperm is now as follows:

- (a) Several Y-genes with complementary effect, similar to the A₁A₂A₃C R series for aleurone color. Of the Y-series, the known genes are Y₁ in chromosome 6, Y₃ in chromosome 2 and probably Y_x of Dr. Brunson, chromosome unknown. The y_x condition is lethal and the y₃ produces albescent seedlings (a₁ gene).
- (b) The Y₅ gene, isolated from Brazilian strains is complementary to Y₁ in producing yellow endosperm but is independent of Y₃ and so, also, of the other Y-genes of the series.
- (c) The Y_D gene (D=determiner) producing the difference orange : yellow, found in Brazilian material and extremely influenced by modifiers. Similar gene found recently by Dr. Jenkins in chromosome 7.
- (d) The B_n gene in chromosome 7, producing yellow pigment only in the aleurone layer. These "lemon yellow" seeds are detectable in stocks lacking one of the complementary Y-genes for endosperm color.

6. The ratio 15 orange : 1 white was secured in one ear resulting from a cross of Brazilian strains orange x white. The plants obtained from the orange seeds were selfed and in 46 ears the following results obtained:

Ears pure for orange	23
Ears segregating 3 orange : 1 white	14
Ears segregating 15 orange : 1 white	9

As the mutation from the recessive to the dominant condition is not probable and the ratio of ears obtained not in favor of two independent genes, some of the plants obtained from the ears segregating 15 : 1 were fixed and will be checked cytologically.

7. The location of the Y₅ gene is being tried and the cross involving a tester of Dr. Randolph's covering most of the chromosomes gave the following results in two ears obtained from the same plant:

Ratio	36		9		19	
Pedigree NO.	Orange (Y ₁ - Y ₃ -)		Yellow (Y ₁ - y ₃ y ₃ Y ₅ -)		White + Lemon yellow	
	+	su ₁	+	su ₁	+	su ₁
179A-1	231	78	69	15	109	48
179A-2	112	28	34	13	37	16
TOTAL	343	106	103	28	146	64

The segregation for su₁ is normal. The yellow seeds not su₁, where the classification was good, were sowed giving most of them al plants. Few plants not al came from Bn seeds since this gene was present in Dr. Randolph's stock. Segregation for bm₂ and cr₁ was normal and only one plant seemed to be gl and none R₈. Proper tests for chromosome 10 are being prepared but we don't know if plant character markers combined with al will be easy to classify.

8. Markers in all chromosomes and in back-ground favorable for the State of S. Paulo (Brazil) and probably for South America conditions are now available. Trisomic stocks for chromosomes 2 to 10 segregating recessive genes in the respective chromosomes are now available and the trisomic segregation will be checked again this summer. The transference of deficiencies in chromosomes 3,4,5,6, and 9 (material from Dr. Stadler) to Brazilian strains is being continued.

9. Treatment of seedlings by artificial light during 15 days and four hours every day, in one very early and other very late stocks did not show significant difference in flowering when compared with plants that did not receive treatment. Also, plants with day-light reduced to 10 hours every day, during 15 days, flowered normally when compared with the control.

E. A. Graner

United States Department of Agriculture
and
Cornell University, Ithaca, N. Y.

1. In the preceding News Letter it was reported that tetraploid hybrids of *Tripsacum* and maize had been produced from experimental autotetraploids of maize pollinated by a natural autotetraploid *Tripsacum* from the Eastern United States. Repeated attempts to obtain seed from these hybrids by backcrossing to the parents failed. Since they produced only aborted pollen, with the possible exception of a very few grains partly filled with reserve food material, extensive attempts to self or sib cross these hybrids were not made. But very recently it was noted that a few partly developed seeds had formed on two of the 13 hybrid plants being wintered over in the greenhouse. These seeds apparently resulted from sib-crossing. By culturing the embryos of these seeds four seedlings have been obtained from which it may be possible to procure additional progenies.

During 1945 an initial attempt was made to repeat the cross of diploid corn and diploid *Tripsacum* made by Mangelsdorf and Reeves in 1930. A diploid *Tripsacum* from Kansas was used rather than the Texas form used by Mangelsdorf and Reeves. Very little difficulty was experienced in making the cross; 35 hybrids each with 28 somatic chromosomes were produced by pollinating 56 ear shoots of corn. The comparable frequency obtained by Mangelsdorf and Reeves was 29 hybrids from 382 ears.

Sporocyte examination of these hybrids is now in progress. The observations to date indicate that there is an appreciable amount of loose pairing at pachytene. Associations of 2, and not infrequently 3 chromosomes are prevalent at diakinesis. However, very few chiasmata apparently are formed as configurations suggesting chiasmata are rare at diakinesis and very few bivalent or trivalent associations persist to the metaphase stage. About one third of the figures have no bivalents on the metaphase plate and most of the other cells have not more than one or two bivalents at this stage.

The meiotic behavior of the chromosomes in these diploid *Tripsacum*-maize hybrids indicates that there has been very little if any exchange of parts of chromosomes during the meiotic prophase. The functioning of any mechanism for the transfer of *Tripsacum* chromatin to corn is conspicuous by its absence. It is quite possible that an occasional exchange of parts between the *Tripsacum* and corn chromosomes may take place as a result of something approaching typical crossing over, or fortuitous translocations; but it would be extremely difficult, on the basis of the observed cytological behavior of the chromosome in these hybrids, to account for a transfer of complete sets of knobs from *Tripsacum* to corn, as postulated by Mangelsdorf and Reeves.

However, the inference to be drawn from the observed meiotic behavior of the chromosomes in the F_1 *Tripsacum*-corn hybrids, namely, that there has been little or no exchange of parts between the corn and *Tripsacum* chromosomes is in full agreement with the observation of Mangelsdorf and Reeves that the plants with no *Tripsacum* chromosomes in the progeny of triploid *Zea*-*Tripsacum* hybrids backcrossed to corn, "were for the most part, normal corn plants differing in no way from ordinary corn plants-----most of the *Zea* chromosomes segregated out intact and completely uncontaminated by their association with those of *Tripsacum*". (M. and R., 1939, pp. 142-143).

2. From a comparison of pachytene figures in different inbred lines it is apparent that consistently "good" figures may be obtained from some lines and consistently "bad" figures from others. Hybrids of good and bad lines have bad figures and plants with good figures are recovered in backcrosses to lines with good figures with a frequency suggesting that a single major recessive gene for good pachytene figures is involved.

Lines having consistently good pachytenes include Lucas Favorite (parent of 29-3 hybrid), 4-8d, L 289, CC5, OS426. Lines with badly clumped pachytenes of poor quality include B 164, OS 420, WF 9, 38-11 and O40B.

The observations on the quality of the pachytene figures were made under a wide variety of climatic conditions in New York and southern California, involving appreciable differences in temperature, humidity, and time of day when fixations were made. The quality of the cytological preparations was remarkably uniform under a wide diversity of environmental conditions.

L. F. Randolph

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H. H. Smith

III SEED STOCKS PROPAGATED

A complete inventory of material on hand was presented in News Letter 14 and additional lists were given in News Letter 16. Inasmuch as there appear to have been relatively few stocks added to the Coop collection since 1941, it has seemed unnecessary to present additional lists. Most of the propagation of material during the past few years has merely involved the growing of cultures from old seed, so that genes would not be lost. However, Dr. Murray began in 1943 to outcross weak genetic stocks to inbreds, in order to make material available in more vigorous combinations. This has been continued and a number of such combinations are ready for use. Progress has also been made in the transfer of marker genes to trisomic stocks.

R. L. Cushing and Rosalind Morris

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Linkage and cytological data on translocations involving chromosomes 1, 2, and 3.

Translocation	Chromo- some	Locus of break	Linkage	Chromo- some	Locus of break	Linkage
1-2b	1	S.2	ts ₂ -P-3.8-T	2	S.6	B-sk-1.4-T
1-2c	1		T-1.4-sr-P	2		near v ₄
1-3a	1	S.25	P-18.7-T-36.9-br	3	L.2	ts ₇ ±2.8
1-3d	1		near br	3		dt±0.6
1-4a	1		br-18.8-T-----bm ₂	4		su±3.0
1-5a	1		br±8.54	5		bm ₁ -T-1.3-pr
1-5b	1		P-24.2-T-30.9-br	5		close to bm ₁
1-5c	1		P-23.0-T-25.3-br	5		bm ₁ ±0.2
1-6c	1	S.3	ts ₂ -P-9.5-T	6	L.2+	very near Y
1-7a	1	L.4	near br	7	L.1+	close to ra
1-7b	1	L.6	br-3.4-T-48.6-bm ₂	7	L.2	T-0.9-ra-gl ₁
1-7c	1	L.3	br±3.9	7	L.1	ra±0.6
1-7d	1	L.8	br-32.4-T-20.4-bm ₂	7	S.4	T-2.9-ra-gl ₁
1-9a	1	S.	P-21.2-T-35.6-br	9	L.	c-wx-11.2-T
1-9b	1	L.6	br±8.9	9	L.5	c-wx-37.8-T
1-9c	1	S.6	ts ₂ -P-0.8-T	9	L.2+	c-wx-12.1-T
1-10a	1	L.4	br±2.7	10	L.3	T-15.3-g-R
2-3b	2		B-v ₄ -4.0-T	3		ts ₄ ±1.1
2-3c	2	S.6	B-0.5-T-4.9-sk	3	S.8	dt±0.2

(Continued)

Translocation	Chromo- some	Locus of break	Linkage	Chromo- some	Locus of break	Linkage
3-5a	3		$ts_4 \pm 2.1$	5		bnl-28.4-pr-6.4-T
3-5b	3	L.	na-4.8-T-19.1-a	5	L	bnl-pr-4.1-T
3-5c	3	L.	na-11.7-T-12.8-a	5	L	T-1.7-pr-bnl
3-6a	3		$ts_4 \pm 1.8$	6		Y-6.6-T-2.8-Pl
3-6b	3	S.8	$dt \pm 0.5$	6	Sat	T-15.6-Y
3-7a	3	S.2	$ts_4 \pm 5.0$	7	L.25	ratl.1
3-7b	3	S.8	$dt \pm 0.4$	7	L.1	near ra
3-7c	3	L.6	close to na	7	L.5	near ra
3-8a	3	L.6	$ts_4 \pm 2.5$	8	L.8	T-13.6-ms8-j
3-8b	3	L.1	close to ts_4	8	L.2	T-32.9-ms8-j
3-9a	3		$ts_4 \pm 2.9$	9	L.1+	c-wx-3.6-T
3-9b	3		lg2-7.9-T-19.3-al	9		c-wx-6.8-T
3-9c	2	L.1	$ts_4 \pm 2.4$	9	L.2	c-wx-7.6-T
3-10a	3	L.1+	$ts_4 \pm 10.4$	10	L.1	T-15.7-g-R
3-10b	3		$ts_4 \pm 1.3$	10		T-18.8-g-R
3-10c	3		$ts_4 \pm 0.7$	10		T-6.5-g-R

E. G. Anderson

MAIZE GENETICS COOPERATION

NEWS LETTER

21

March 1, 1947

The data presented here are not to be used in
publications without the consent of the authors.

Department of Plant Breeding
Cornell University
Ithaca, N. Y.

MAIZE GENETICS COÖPERATION
DEPARTMENT OF PLANT BREEDING
CORNELL UNIVERSITY
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December 26, 1946

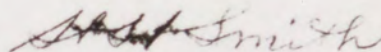
To Maize Geneticists :-

This is a call for material for the 1947 Maize Co-op News Letter. The dead line on contributions is February 15.

Since there have been many changes in personnel following the war your cooperation is requested in correcting any errors in mailing addresses and suggesting names of interested investigators who may not be on our present list.

Comments: The Maize Genetics Cooperation has received a generous grant from the Rockefeller Foundation to continue operation. Mr. James. E. Wright, Jr. has been enrolled for part time student help. Requests for seed of our genetic stocks has shown an upward trend.

Sincerely yours,



H. H. Smith

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Ed. note: A change in size of page from previous
issues was necessitated by a shortage of
mimeograph paper.

I. REPORTS FROM COÖPERATORS

California Institute of Technology
Pasadena, California

Alignment of translocations on chromosome 2.

Translocation	Cytological position	Linkage	Number of plants
2-3a		near lg ₁	Burnham
2-6b	S.75	gl ₂ -3.9-T-0.9-B	2008, 3152
2-3c	S.65	B-0.5-T-4.9-sk	3317, 183
1-2b	S.6	B-5.3-T-1.4-sk	1176, 1176
2-9a	S.65	sk±0.5	784
2-3d	S	sk-8.5-T-12.5-v ₄	447, 939
2-9b	S.1	ts ₁ -5.0-T-7.8-v ₄	662, 1542
2-5a	L.1	T-7.3-v ₄	Rhoades
2-4d	L	ts ₁ -9.6-T-8.8-v ₄	125, 1059
2-5b	L	T-5.0-v ₄	185
2-10a	L.2	ts ₁ -13.5-T-6.5-v ₄	384, 1145
2-7b	L.25	ts ₁ -15.3-T-5.4-v ₄	470, 1091
2-6d	L.3-	ts ₁ -26.6-T-4.2-v ₄	403, 754
2-6c	L.3	ts ₁ -12.3-T-1.7-v ₄	594, 1869
1-2(17)		ts ₁ -10.7-T-1.1-v ₄	375, 481
2-4a	L.3	ts ₁ -12.9-T-1.0-v ₄	395, 1522
1-2c	L.3	ts ₁ -8.5-T-0.3-v ₄	649, 1164
2-6a	L.3	v ₄ ±1.1	354
2-7c	L.3+	ts ₁ -v ₄ -1.0-T	592
2-3b		ts ₁ -v ₄ -4.0-T	1412
2-4b	L.6	ts ₁ -v ₄ -5.6-T	1207
2-4c	L.8	v ₄ -19.0-T-34.2-ch	1098, 1317
2-4(a-29)		v ₄ -22.3-T	622
Inv.	L.7+	v ₄ -34.5-T-30.4-ch	447, 447

E. G. Anderson

Ira W. Clokey

California Institute of Technology, Pasadena, California

Linkage and cytological data on translocations, to add to the list reported in the 1946 News Letter, pages 34 and 35

Translocation	Chromo- some	Locus of break	Linkage	Chromo- some	Locus of break	Linkage
2-3d	2	S.	sk-8.5-T-12.5-v ₄	3	L.	na-13.0-T-7.1-a
2-4a	2	L.3	ts ₁ -12.9-T-10-v ₄	4	L.2	su-3.3-T-14.0-Tu
2-4b	2	L.6	ts ₁ -v ₄ -5.6-T	4	L.4	Tu-gl ₃ -15.0-T
2-4c	2	L.8	v ₄ -19.0-T-34.2-ch	4	S.1	su-9.1-T-30.8-Tu
2-4d	2	L	ts ₁ -9.6-T-8.8-v ₄	4		near Tu
2-4(a-29)	2	L	ts ₁ -v ₄ -22.3-T	4		su-5.6-T-18.8-Tu
2-5a	2	L.1	B-T-7.3-v ₄	5	S.1	T-1.5-bm ₁ -pr
2-5b	2	L	B-T-5.0-v ₄	5		bm ₁ tl.
2-6a	2	L.3	v ₄ tl.1	6	S.1	T-9.6-P1-sm
2-6b	2	S.75	gl ₂ -3.9-T-0.9-B	6	L.65	Pl-sm-3.3-T
2-6c	2	L.3	ts ₁ -12.3-T-1.7-v ₄	6	L.3	near Y
2-6d	2	L.3	ts ₁ -26.6-T-1.1-v ₄	6	L.3	near x
2-7b	2	L.25	ts ₁ -15.3-T-5.4-v ₄	7	L.2	T-1.3-ra-gl ₁
2-7c	2	L.3	ts ₁ -v ₄ -1.0-T	7	L.1+	T-5.7-ra-gl ₁
2-9a	2	S.65	sk±0.5	9	L.65	C-wx-30.7-T
2-9b	2	S.1	ts ₁ -5.0-T-7.8-v ₄	9	L.2	C-wx-7.5-T
2-10a	2	L.2	ts ₁ -13.5-T-6.5-v ₄	10	L.7	T-1.9-g-R

E. G. Anderson

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New York, New York

1. A new mutable gene.

Mutable alleles have been found at the P, Bt, and Wx loci. These mutable alleles may be described as recessives with a high mutation rate to the dominant allele. In addition there is the genically induced mutability of recessive a by the Dt gene. The effect of Bh on recessive c probably belongs in this category. A new type of mutable allele has recently been found. A dominant A allele mutates with high frequency in both somatic and germinal tissue to an intermediate allele producing light aleurone color and red-brownish plant color. The effect on pericarp color has not yet been determined. An example of the mutation rate of this mutable A allele (designated A^m) is as follows: The cross of a x A^m gave 74 kernels with self-colored aleurone, 61 kernels mosaic for deep and light colored aleurone, and 24 with light colored aleurone. At least two different intermediate alleles, differing in intensity of color in aleurone and plant, have been found.

2. Directed segregation.

A derived strain from a complex translocation involving chromosomes 5 and 3 has the following constitution: Nine normal bivalents, including chromosome 5, and a chain of three consisting of a normal chromosome 3, a short arm, and a long arm of chromosome 3. When this chain of three is present in plants with a certain genetic background, the orientation of the chain on the metaphase I spindle is approximately random, i.e., orientation of the chain leading to alternate segregation of the three members and giving euploid combinations occurs in 50 per cent of the P.M.C., while a linear orientation leading to aneuploid gametes occurs in 50 per cent of the P.M.C. In other strains, differing in genetic modifiers from the above, the orientation of the chain is such that in about 95 per cent of the cells the normal chromosome 3 passes to one pole while the other two members of the chain pass together to the other pole. Here we apparently have a case of genic control of orientation, and hence segregation. This finding is of interest in connection with the breeding behavior of *Oenothera* translocations.

3. Maize strains with 11 bivalents.

From the translocation mentioned above it has been possible to obtain plants with 11 pairs of chromosomes. They carry no duplication of genetically active chromatin. This increase in chromosome number was a consequence of the breaking of the centromere of chromosome 3 into two portions with both the short and long arms receiving part of the parental centromere.

M. M. Rhoades

New allele of Ga_1 on chromosome 4.

In the course of studies on a new chlorophyll striping character, a super-allele of Ga_1 on chromosome 4, was found. This allele, Ga^S , is dominant over Ga . Small ga pollen does not function on Ga^S silk even in the absence of competition with Ga or Ga^S pollen. Out of 14 such crosses only one seed developed on one ear. The other 13 ears were completely devoid of seeds. This is interesting in view of the fact that ga pollen does function on Ga silk when there is no competition with Ga pollen. Selfing of plants heterozygous for Ga and Ga^S using sugary as a marker, $Ga\ su/Ga^S\ Su$, showed that Ga^S pollen functions in the production of approximately 66 per cent of the kernels when competing on Ga^S silk. This super-allele appears to be independent of the striping.

Drew Schwartz

Studies with mutable waxy.

An allele at the waxy locus (wx^m), which mutates with a high frequency to Wx in both endosperm and germinal tissue, is under investigation. This allele is intermediate between Wx and wx^S ; $Wxwx^m$ plants segregate approximately 3 Wx :1 wx^m ; and wx^mwx^S plants approximately 3 wx^m :1 wx^S . (Ratios deviate from 3:1 in some cases due to germinal mutations.)

Typically, a wx^mwx^S plant when selfed gives three classes of kernels: About 1/4 waxy, less than 3/4 mosaic (waxy with various sized spots of normal starch), and a variable number (often 5-20 per cent) of kernels with normal starch endosperm.

The most readily observable mutation both somatically and germinally is from wx^m to Wx . Mutation rate comparisons made between different stocks by counting the numbers of Wx kernels produced in crosses wx^mwx^m backcrossed or selfed, indicate differences of the following order of magnitude:

	wx^m	Wx	wx^S	% Wx
S-43-12 selfed	140	4	1	2.7%
S-47-2 x wx^S	199	41		17.0
9903-10 selfed	63	24		27.5
9903-4 selfed	53	34		39.0

The mutable allele probably also mutates to wx^S . Four ears from a cross wx^Swx^S x wx^mwx^m threw 5.3 per cent wx^S seed. A mosaic kernel when grown and selfed gave the phenotypic ratio 29 Wx :212 wx^m ; 19 wx^S - the 29 Wx and 19 wx^S kernels arising by mutation. These seeds are being grown now to establish their genotype.

In a few stocks, kernels have been found consisting entirely of normal starch except for many small scattered waxy spots. Since in

these cases the rest of the ear bore all normal starch kernels (Wx by mutation), these spotted kernels may represent reverse somatic mutations of a somewhat unstable Wx' allele back to wx.

A study of the distribution of Wx and wx pollen grains in alcohol preserved tassels from wx^mwx^m plants (Wx grains stain blue and waxy stain red with weak IKI) indicates that mutations may occur so early in tassel development as to affect an entire branch, or even a few neighboring branches. On the other hand, some branches carry anthers segregating in varying ratios, indicating later mutations. Mapping of ears from crosses wx^mwx^m x wx^swx^s has not revealed any sector pattern as yet.

Ruth Sager

Connecticut Agricultural Experiment Station
New Haven, Connecticut

Varieties of corn grown in the Northeast and in the Middle West at the same latitude are noticeably taller in the East. Several environmental conditions are involved in this growth difference, principally light intensity and temperature. Plants of many species, including maize, grown under tobacco shade cloth are significantly taller and broader in leaf than plants from the same lots of seed grown in full sunlight. Under the cloth shade the temperature is the same as outside but the humidity is higher and the light intensity is lower. The same effect is noticed in the field where short-stalked varieties of corn are grown in single rows between taller varieties. Where there is a wide alley between ranges the plants at the ends of the rows are shorter than those in the center of the rows, the plants graduating in height. Here humidity and temperature are the same but light intensity varies.

Some corn seedlings started in the greenhouse and set outdoors were shorter at maturity than plants from the same seed started outdoors. This indicated that temperature in the early stages of growth had an effect. To test this, seeds of a uniform, vigorous, first generation hybrid (Wf9 x P8) were germinated in an incubator at about 30° C. until the shoots and roots were from one fourth to one half inch long. Three different lots of sprouted seedlings, were held at 40, 50 and 60° C. for one hour. They were then planted in pots and left in the greenhouse until it was certain the plants would grow. They were then set in the field alongside plants from the same lot of seed sown in the open ground at the same time the treated seedlings were started in the incubator. Some of the treated seedlings died but enough were started in each lot and later thinned to give an even stand of plants in the field.

All three lots of heat-treated seedlings were shorter in height, less vigorous in growth throughout the season and later in flowering than the treated plants. All lots grew to full maturity and were measured after growth had ceased. The results are: Control 101: 40° C. 87; 50° C. 89; 60° C. 93 inches in height. The differences between the three

temperature treatments are small. All three averaged 90 compared to 101 inches in height for the control.

The result that was not anticipated was the pollen sterility in all treated lots. Normal tassels were produced with well-developed florets but the anthers were small and shriveled and for the most part remained enclosed in the glumes. In view of the fact that high temperatures sterilize the male germ cells in animals, from amphibians to mammals, these results are highly significant. This influence on growth is an anti-vernalization effect and may have wide usefulness in the production of hybrid seed especially if shown by other plants as well as maize.

D. F. Jones

A second "Teopod" mutation.

Another mutation to Teopod or a similar character, has occurred. This mutant was discovered by Dr. Bailey Pepper of the New Jersey Experiment Station in a field of sweet corn growing in New Jersey. We obtained seed from Dr. C. M. Haensler of the New Jersey Station. It was grown under the name of "Corn Grass" because it was much more like a grass than normal corn. The blades of the leaves are narrow and there are many tillers giving a grassy appearance. In the field the plants do not exceed three feet in height and look much less like normal corn than the Teopod of Lindstrom. However until the two stocks have been tested by crossing it is not possible to state whether they are allelic. These tests will be made in 1947.

The "second Teopod" was first grown in Connecticut in 1945. Seed from the mutant produced two kinds of plants, normal and Teopod, in approximately equal numbers. The normal plants were recessive. Open-pollinated seed from the Teopod plants gave in 1946 a 1:1 ratio for normal and Teopod. In the field in 1945 and 1946 no tassels of any kind were produced. The stock has been maintained by backcrossing to normal corn.

In the 1946-1947 greenhouse, crop grown under a shorter day, tassels with apparently good pollen have been produced.

The "Teopod" reported here makes many brace roots beneath the leaf sheaths. Some of these grow to be several inches in length. It occurred to us we might propagate these asexually and an attempt was made. The cut stalks rooted and lived for several weeks. Had the attempt been made earlier in the summer, it is possible they might have been successful.

One is forced to speculate whether mutations to such bizarre types as Teopod may have any bearing on the origin of corn. If a single gene can change the habit of a corn plant so completely, might not a reverse mutation have originally occurred to give us normal corn? Possibly the ancestor of maize may have been something more like one of the Teopods.

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The relation of plant colors to total dry weight in maize.

A number of years ago Brink (Jour. Amer. Soc. Agron. 26: 697-703, 1934) reported the relative yielding capacity of four different anthocyanin plant-color types, namely, purple A B Pl, sun red A B pl, dilute purple A b Pl, and dilute sun red A b pl. The stocks were so bred that all four classes occurred with approximately equal numbers in each of the 11 families involved in the test and so that the residual genotypes of the four color classes were approximately the same. Somewhat more than 3500 plants were observed and yields were reported as average dry weight of ears per plant in pounds as follows: Purple .433, sun red .569, dilute purple .561, dilute sun red .511. Thus dilute sun red, the prevailing color type of the country, yielded significantly more than purple and both sun red and dilute purple significantly more than dilute sun red.

The writer has made similar tests, using total dry weight of plant as the criterion of yield. The genes b and pl were derived from two dilute sun red (A b pl) inbred dent lines and their dominant alleles from several genetic stocks, including purple A B Pl, brown a B Pl, and reddish brown a^P B Pl. Each of these genetic stocks was crossed with each dilute sun red inbred and purple plants of the resulting progenies were backcrossed from one to three times with the same or the alternate inbred. Some of the cultures, therefore, were little if any more vigorous than the inbred lines and some showed marked heterosis. The four color types of any one culture, however, were comparable and occurred in approximately equal numbers. In table 1 are shown the average dry weights per plant in grams for the several color types of each of 14 cultures.

Table 1

Culture number	Number of plants	Mean dry weight per plant			
		<u>A B Pl</u>	<u>A B pl</u>	<u>A b Pl</u>	<u>A b pl</u>
1	90	142	111	98	110
2	76	129	132	129	110
3	91	165	163	150	145
4	92	133	145	145	127
5	93	206	217	229	184
6	73	78	82	118	78
7	96	204	229	222	230
8	89	161	162	146	150
9	89	118	103	122	104
10	89	187	207	227	222
11	74	117	122	115	117
12	76	68	88	77	74
13	96	202	181	186	199
14	94	186	172	185	203
Total	1218				
Average of mean dry weights		150	151	153	147

In addition to backcrossing heterozygous purple plants of table 1, certain sun red and dilute purple plants were backcrossed with one or other of the same dilute sun red inbreds. Results are shown in table 2.

Table 2

Culture number	Number of plants	Mean dry weight per plant			
		<u>A B pl</u>	<u>A b pl</u>	<u>A b Pl</u>	<u>A b pl</u>
15	76	143	110		
16	89	129	124		
17	86	128	134		
18	80	123	110		
19	82	132	128		
20	79	108	103		
21	91	222	238		
22	95	195	192		
23	94	201	194		
24	95	195	217		
25	88	120	106		
26	83	72	75		
27	92	259	251		
28	92	206	201		
Total	1222				
Average of mean dry weights		160	156		
29	84			143	146
30	91			149	152
31	89			166	153
32	72			136	113
33	75			157	113
34	80			140	120
35	74			126	118
36	61			71	85
37	92			253	254
38	94			199	199
39	72			196	171
40	31			202	184
41	26			215	209
Total	941				
Average of mean dry weights				166	155

From the results presented in table 1, it is obvious that purple plants were not appreciably less in dry weight than sun red and dilute purple plants. The dilute sun red plants were lowest in dry weight but not markedly less than the other three color types. The results given in table 2 were similar to those of table 1. In one lot of cultures, dilute sun red plants were slightly less in weight than sun red ones. In the second lot of cultures, dilute sun red again was less in weight than dilute purple; and the difference here is greater than in the other tests.

On the whole and in so far as the results here reported are concerned, it can be said that in segregating cultures, dilute sun red plants were slightly less in total dry weight than were plants of the other color types. Whether or not the fact has any significance, it should be remembered that, in all these tests, comparisons have been made between homozygous dilute sun red and heterozygous purple, sun red, and dilute purple.

Among genes other than B and Pl that are related to plant colors of maize, the A pair is of fundamental importance. In most instances, only in the presence of dominant A do anthocyanin pigments develop. Where A results in purple or red, its recessive alleles usually give brown or have no appreciable effect on color. Accordingly several tests have been made of the possible influence of A and of some of its alleles on dry weight of plant. Certain colorless (green) types were crossed with the two dilute sun red inbreds used in the tests noted above. The F_1 plants were backcrossed to the colorless parent. Three sets of cultures were grown from the following crosses: (a B pl x A b pl) x a B pl, (a b Pl x A b pl) x a b Pl, and (a b pl x A b pl) x a b pl. In each set of cultures, two color types were represented. The results are given in table 3.

The records of table 3 reveal small but not consistent differences in total dry weight of plant between colored and colorless individuals of the several cultures. In averages of mean dry weights, sun red plants were about five per cent lighter than the corresponding colorless ones, while dilute purple and dilute sun red plants were heavier than their colorless sibs by six and three per cent, respectively. With the genotypic backgrounds here involved, there was relatively little effect of A and of its recessive allele a on total dry weight of plant.

There remains to be considered a possible difference between the influence of A and of some of its recessive alleles when the background genotype contains both dominant B and dominant Pl. In one lot of tests purple A B Pl was crossed with brown a B Pl and backcrossed once with the same brown. The results are recorded in the first section of table 4. Another allele of A, namely, aP, gives a reddish brown plant when in combination with B and Pl. Reddish brown was crossed with one of the two dilute sun red inbreds and the purple plants resulting were backcrossed once or twice with the same reddish brown. Recessive a2 with B and Pl gives brown plant color. This brown was crossed with reddish brown and the resulting purple F_1 plants were backcrossed with reddish brown. The genotypes concerned here are as follows: (A a2 B Pl x aP A2 B Pl) x aP A2 B Pl. All these progenies, segregating purple and reddish brown, are recorded in the second section of table 4.

Table 3

Culture number	Number of plants	Mean dry weight per plant					
		<u>A B pl</u>	<u>a B pl</u>	<u>A b Pl</u>	<u>a b Pl</u>	<u>A b pl</u>	<u>a b pl</u>
42	83	150	157				
43	73	158	138				
44	88	162	163				
45	70	176	180				
46	81	159	169				
47	88	182	215				
48	78	210	221				
49	52	189	227				
50	65	184	196				
51	57	188	193				
Total	735						
Average of mean dry weights		176	186				
52	47			144	130		
53	37			171	170		
54	42			143	105		
55	69			186	175		
56	73			171	163		
57	76			165	167		
58	79			169	163		
59	70			193	158		
60	70			166	183		
61	70			174	169		
Total	633						
Average of mean dry weights				168	158		
62	71					185	195
63	63					180	170
64	37					181	155
65	60					146	158
66	57					171	174
67	48					172	162
68	51					146	137
69	57					132	139
70	46					181	159
71	59					167	164
Total	549						
Average of mean dry weights						166	161

Table 4

Culture number	Number of plants	Mean dry weight per plant					
		<u>A B Pl</u>	<u>a B Pl</u>	<u>A B Pl</u>	<u>a^p B Pl</u>	<u>A2 B Pl</u>	<u>a2 B Pl</u>
72	48	150	134				
73	80	95	75				
74	83	109	96				
75	<u>80</u>	97	88				
Total	291						
Average of mean dry weights		113	98				
76	61			126	96		
77	61			119	81		
78	71			111	84		
79	61			115	85		
80	49			156	138		
81	40			128	115		
82	81			112	89		
83	63			142	114		
84	56			126	122		
85	66			140	101		
86	<u>76</u>			157	106		
Total	685						
Average of mean dry weights				130	103		
87	59					167	141
88	68					170	128
89	41					173	147
90	45					162	119
91	75					154	127
92	67					163	117
93	83					171	124
94	92					136	135
95	73					140	103
96	77					117	95
97	73					207	182
98	67					140	91
99	<u>78</u>					172	131
Total	898						
Average of mean dry weights						159	126

Brown plants of the genotype A a2 B Pl were crossed with one of the dilute sun red inbreds, with purple, and with reddish brown. In all instances the resulting F_1 purple plants were backcrossed with A a2 B Pl. Here then the brown plant color is conditioned not by an allele of A but by an allele of A2. The cultures involving A2 and a2 are listed in the third section of table 4.

Cultures segregating for purple and brown plant color, as shown in table 4, whether the brown color is conditioned by a, or its allele aP, or by a gene of a different chromosome a2, all exhibit consistent results. The averages of the mean dry weights are greater in each of the three lots of cultures by from 15 to 26 per cent for the purple than for the brown plants. Moreover in each of the 28 cultures of table 4 without a single exception, the purple plants are heavier than the brown ones.

Since for one of the genes conditioning brown plant color, namely, a, no consistent effect on weight was found when A and a were combined with B pl, b Pl, and b pl (table 3), it seems reasonable to assume that the lighter weight of brown plants conditioned by a, aP, or a2 in contrast with purple plants conditioned by the dominant alleles of these genes, results from some deleterious effect of the brown pigments in the physiology of the plant, rather than from a direct effect of the recessive genes or of growth factors closely linked with them.

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Mendelian interpretation of offspring-parent regressions.

Dr. K. Mather on his recent visit to this country discussed some extensions of methods proposed by Fisher, Immer and Tedin, (Genetic 1932), for estimation of dominance bias in quantitative inheritance.

My own attack in the last News Letter is also an extension of the same. My approach seems to have some advantages from employing highly inbred or homozygous parents. Uncertainty on linkage effects is largely eliminated. Dominance does not reduce correlation between phenotypes of homozygous parents and the gametes they produce. I have found no particular advantage in requiring equal frequency of a and A alleles by confining study to populations which stem from a single selfed heterozygote in each case. Samples of homozygous lines, selected or otherwise, seem to be satisfactory. If all of this be true the method must have a wide utility and may be presented again from more of a Mendelian and less of a mathematical viewpoint.

If the heterozygote aAbBcCdD is crossed to the multiple recessive tester aabbccdd, testcross progeny may be classified on kinds and frequencies of four distinct qualitative characters to obtain a reflected view of dominant alleles in gametes of the heterozygote. This is the

method of classical genetics. It has been seldom noted here that regression of number of plus characters in testcross progeny on number of dominant alleles in parent gamete is 1.0. Every plus allele in a gamete provides a plus character in the zygote, regardless of linkage.

The top dominant AABBCDD is clearly worthless as a tester. Offspring-parent regression is zero. Intermediate testers are efficient in inverse proportion to the number or proportion of loci of AA type. Thus if testers in general are of aa type at one half of the loci which are heterozygous in the F_1 to be analyzed, a dominant allele in F_1 gametes will provide a dominant character in testcross progeny in one half of the cases. In the other half the dominant character is always provided by the tester and a dominant allele in the F_1 gamete can add nothing more. Regression is one half. Reduction of regression by dominant genes in the tester is purely a dominance effect. This dominance effect is reduced one half by selfing the testcrosses.

It hardly seems necessary to labor with the transfer of these concepts to the general field of multigenic inheritance where effects of the several genes combine in a single quantitative measure, and where dominance is taken into account quantitatively. In the former case, concern is primarily with frequencies. Basic effects of genes and dominance effects are both tacitly defined as unity throughout. In the latter case the two effects must be defined separately and quantitatively. We cannot assume that either is unity since we are concerned with degree of expression, not with just whether the character is or is not expressed.

In my attack the array of F_1 gametes is replaced with an array of gametes from an array of homozygous parents. The purpose is no longer to obtain a reflected picture of the gametic array. That array is already revealed in the array of homozygous parents. The purpose now is to estimate regressions of testcross progeny on gamete or homozygous parent with different testers. If both the bottom recessive and top dominant were available as testers, decline in regression from one case to the other would reveal directly the average degree of dominance. But neither of those two testers is likely to be available in multigenic cases. We are restricted to a study of regression relations with such testers as we may be able to develop.

For quantitative definitions of basic gene effects and dominance effects we may well employ the general scheme of Fisher, et al (1932) which is essentially that of Fisher in his 1918 paper on correlation between relatives, and of Mather on his recent visit. If the basic, phenotypic effect of substituting A for a is "d", phenotypes of aa, aA, AA are 0, d, 2d. The heterozygote is strictly intermediate. But if there is in addition an interaction of a with A to provide also a dominance effect "kd", the phenotypes are 0, d+kd, 2d. These quantities are deviations from a working origin at aa. Deviation of the heterozygote from strict intermediacy is kd, (h in the notation of Fisher, et al).

For a multiple set of genes $a_1A_1, a_2A_2 - - - a_nA_n$, we may as well let d and kd be average values for the several loci. Then if gene action is additive each genotype is evaluated (estimated) by summing the

several d's and kd's. The simplest case is $n = 2$. The checkerboard frame is

P_2	$4d$	A_1A_2	$2d$ $2kd$	$3d$ kd	$3d$ kd	$4d$ 0
		a_1A_2	d kd	$2d$ $2kd$	$2d$ 0	$3d$ kd
	$2d$	A_1a_2	d kd	$2d$ 0	$2d$ $2kd$	$3d$ kd
	0	a_1a_2	0 0	0 kd	d kd	$2d$ $2kd$
			a_1a_2	A_1a_2	a_1A_2	A_1A_2
			0	$2d$	$4d$	
			P_1			

Table 1 -

Phenotypes of the 3 parent classes are written on the margins along with the gametes of each class. Phenotypes alone are written in interior cells for offspring. It may be desirable in teaching to write genotypes also in the cells and to evaluate some of them by counting a d for each A allele and a kd for each aa locus or each interaction of unlike alleles. It may also be desirable to write genotypes of parents and evaluate them, noting absence of dominance effects.

Table 1 is a simple regression surface. Our avowed purpose is to study the effect of k on the shape of the surface that we may interpret shapes of data surfaces in terms of k, average degree of dominance.

In practice the homozygotes $a_1a_1 A_2A_2$ and $A_1A_1 a_2a_2$ are ordinarily indistinguishable. This means that the two center columns and two center rows of table 1 may as well be pooled to conform with the situation of data on a quantitative character. Pooling provides,

P_2	4d	2d 2kd	3d kd	4d 0
	2d	d kd	2d kd	3d kd
	0	0 0	d kd	2d 2kd
		0	2d	4d
		P_1		

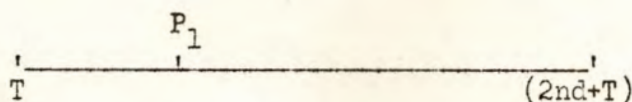
Table 2 -

Note that the entry in the central cell, e.g., of table 2 is the mean of the four central cells of table 1. It is the predicted (average) result of crosses of homozygotes of the types indicated on the margins. Deviations of the four crosses from the mean are deviations from regression due entirely to dominance, to variations in degree of heterozygosity, specific combining ability. These variations are not predictable from data on the parents. The teacher should write frequency distributions of individual crosses in each cell of table 2 along with the means given here.

Note further that, while tables 1 and 2 represent two-factor checkerboards of classical genetics with gametes of F_1 recorded on the margins and F_2 phenotypes in interior cells, the view here is arrays of homozygous lines on the margins with F_1 phenotypes of crosses of such lines in cells of the tables. Subsequently, interior values will be referred to as F_1 s in agreement with modern corn breeding practice. The two situations are strictly analogous only when a and A are equally frequent in the sample of homozygous parents.

If table 2 is expanded to include many loci, parent values are 0, 2d, 4d, - - - - 2nd. A statement of the mean F_1 of any cell in terms of parent values would be the general regression function of F_1 on P_1 and P_2 . The solution of this problem was given in the previous News Letter. The mean of any cell in a table of the type of table 2, may be calculated by solving a smaller checkerboard. Detailed arrays of gametes of the two parent types are written on the margins. But this is merely taking the product of two gametic arrays, a fundamental principle of Mendelism. Hence, if u and w are the proportions of loci AA in P_1 and P_2 respectively, gametic arrays are represented in general by $(1-u)a + uA$ and $(1-w)a + wA$. In all of the crosses of P_1 type parents \times P_2 type parents together, expectations are $(1-u)(1-w)aa$, $[u(1-w) + w(1-u)] aA$, $uwAA$. The sum of these three proportions, each multiplied by n and by the respective phenotypes 0, d+kd, 2d, is the expected increment of mean F_1 over the multiple recessive T. Making the substitutions $u = (P_1 - T)/2nd$ and $w = (P_2 - T)/2nd$ provides the desired function.

The concept $u = (P_1 - T)/2nd$ might be presented effectively to a class by laying off an arbitrary scale to represent the range of phenotype from



bottom recessive to top dominant. The scheme is to count $2d$ for each locus AA as the increment above T , hence, $2nd$ where all n loci are AA . The position of any homozygote P_1 on this scale reveals directly the proportion of loci AA in P_1 , $u = (P_1 - T)/2nd$.

The purpose of T is to adjust for the possibility that the phenotype of the bottom recessive is not zero on the data scale.

It is instructive to verify from table 2 results reported last year. The left column may represent a series of hybrids having a common parent P_1 , the tester, which is aa at each locus. Lines being tested are represented on the parallel margin as different values of the variable P_2 . It is clear that if the tester is completely recessive, every substitution of AA for aa in P_2 will provide a substitution of aA for aa in F_1 . Regression of F_1 on P_2 is $(aA - aa)/(AA - aa)$ or (one basic gene effect plus one dominance effect)/(two basic effects) or $(1+k)/2$. Note that the increment from one cell to the next, left column of table 2, is $d+kd$ and that the corresponding increment in the P_2 column is $2d$. The ratio is $(1+k)/2$. When P_1 is aa throughout $P_1 - T = 0$. Substitute in last year's formula for bp to obtain $bp = (1+k)/2$, if $P_1 - T = 0$.

Similarly from the right column of table 2, $bp = (1-k)/2$, when P_1 is AA throughout, $(P_1 - T) = 2nd$. Expansion of table 2 to include many loci will not provide different results.

If, as in most actual cases, some proportion u of the loci of P_1 is AA and $1-u$ is aa , the weighted mean increment of F_1 is $[n(1-u)(d+kd) + nu(d-kd)]/n$. Or the weighted mean of slopes is $(1-u)(1+k)/2 + u(1-k)/2 = (1+k)/2 - uk$. Substituting $u = (P_1 - T)/2nd$, $bp = (1+k)/2 - (k/2nd)(P_1 - T)$.

If bp is $(1+k)/2$ in the left column of table 2 and $(1-k)/2$ in the right column the increment of bp across the table is $[(1-k) - (1+k)]/2 = -k$. The concurrent increment of u is 1 , and of P_1 it is $2nd$. Regression of bp on u is $-k$ and on P_1 it is $-k/2nd$, as the formula $bp = (1+k)/2 - (k/2nd)(P_1 - T)$ expressly states.

Thus, the values reported last year may be verified and their interpretations clarified by direct inspection of table 2.

If it is not immediately obvious that the regression estimates are unaffected by linkage and by relative frequencies of a and A alleles, except as noted, the student may need to work out some specific examples with numerical values assigned to d , kd , q , and per cent crossover and calculate regressions by machine formulas as well as by direct substitution in present formulas.

It is also clear that bp for the midcolumn or midrow of table 2 is one half, and that mean bp for all three columns or all three rows is one half. This latter case of mean bp for the whole table is the one usually calculated for regression of offspring on one parent. If a and A alleles are equally frequent, frequencies of the three columns are expected in the ratio 1:2:1 and dominance effects on regression are effectively cancelled. Note that bp is always one half if $k = 0$. But if a alleles are in the minority, the frequency of the right column will be greater than that of the left column and expectation is that dominance will depress mean partial regression below one half. This seems to be an adequate explanation of low regressions of yields of corn hybrids on yields of inbred parents. No alternative explanations of higher order interactions of genes or of inefficient plot technic appear to be necessary.

The function, $F_1 = b_1aP_1 + b_1bP_2 + b_2P_1P_2 + C$ may be fitted to data on samples of homozygous parents and the several F_1 crosses, or F_2 by selfing F_1 . For F_1 data, estimates of b_1 are estimates of $(1+k+kT/nd)/2$, on the assumption of additive gene action. Estimates of b_2 are estimates of $-k/2nd$. Regression of bp on P_1 or on P_2 is the same estimate of $-k/2nd$.

As indicated last year, the general regression function may be solved to obtain estimates of bottom recessive, top dominant, and average degree of dominance. From the regression of bp on P_1 , the estimate of P_1 for $bp = 0$ may be obtained. This is the critical value of P_1 . Such a tester combines equally well with poor, medium and good lines on the average. Better testers may be expected to combine better with low lines than with high lines, bp is negative.

The several estimates reported last year are in all respects surprisingly consistent with the hypothesis of overdominance in vigor of corn. Tests of significance of b_2 reported last year are apparently in error. The appropriate test is for significance of departure from linear regression (Snedecor 14.3). By this test no single estimate of b_2 is significantly different from zero which may mean merely that numbers are too small. The crucial point for overdominance is whether k is significantly greater than 1. An additional set of data from C. M. Woodworth, Oren Bolin and Earl R. Leng of the Illinois Experiment Station gives essentially the same picture. The critical value of P_1 is 4.4 bu./A. Yields of inbred parents range from 2 to 40. Mean yield of F_1 s is 103.

We have then one more set of data consistent with the others in supporting the conclusion that the more vigorous inbred lines in hand are worthless or worse as testers for general combining ability, since bp is zero or negative with such lines as testers.

That the few sets of data are not crucial for overdominance is not surprising. They would not be crucial even if the test for k greater than 1 showed high significance in each case. So few cases of monogenic inheritance and linkage would not prove the chromosome theory of heredity. When many more sets of data on different types of characters in both cross- and self-fertilized species have been analyzed we may have a clearer picture of where and to what extent dominance bias occurs. But even then

the results can hardly be conclusive and we will probably still need to be content with theories which agree best with the whole body of evidence.

There is a suggestion in corn yield data that the relative order of rank within either a group of inbred lines or within a group of hybrids may be quite different in two different environments. Further, the shape of the fitted regression surface may also vary greatly in response to environmental effects. If alleles A' and A perform different functions in the sense of East, $A'A'$ may be usually inferior but sometimes superior to AA . The heterozygote $A'A$ if better buffered to environmental shifts may be on the average superior to either homozygote. In these events, A will probably be the more frequent and also the dominant favorable in the usual environment. But the possibility exists that in some environments A' will be the dominant favorable, with dominance still in the direction of greater vigor. The dominant favorable A' will be in low frequency. The ratio k of an average dominance effect to an average basic effect may be changed and with it the equilibrium gene frequency ratio. All of these shifts will be likely to appear in the regression analyses for a given sample of stable lines and F_1 s in different environments.

Fred H. Hull

Addendum.

Since the above report was typed I have received from Dr. Paul H. Harvey yield records on 12 lines and the 66 F_1 s and have now completed the first part of the analysis. Yields of lines (selfed four times) ranged from 12 to 24 bu./A. Mean F_1 is 46. The critical value of P is 25, one bushel above the top line. These data seem to agree with the other sets and the conclusions drawn from them in all respects.

These last results have given me sufficient confidence to propose a further attack for which a considerable body of data is now available, - data on F_1 s but not on the parent lines. Mean F_1 for any column of table 2 may be considered a measure of the general combining ability G of the constant parent for that column. It is easily demonstrated that G is a linear function of P . Hence, we may as well estimate the G value of a tester which provides zero partial regression of F_1 on G . Where the several F_1 s of a group of lines have been tested in as many as four replications, one half of the replications may be employed to estimate G values for the lines. The remaining replications may estimate F_1 s. Correlation of experimental errors in the two estimates are thus eliminated. The analysis, as before, is to run the simple regression of each F_1 column on the parallel column of G ; then to run the simple regression of the first order regressions on G values of the respective constant parents; and finally to estimate G for $b_p = 0$. If this critical value of G is within the range of the data the only direct interpretation I have found is overdominance.

This kind of analysis has been run with the data on Late Yellow Single Crosses from the cooperative tests of the U.S. Department of

Agriculture with Ohio, Indiana, Illinois, Kansas, Nebraska and Oklahoma in 1943. Mean G for each line was based on the data of five states for analysis with F_1 data of the sixth state in each case. The critical value of G is below the G measure of the top line in three cases and slightly above in two cases. In the sixth case the trend of regression is upward and the data are apparently not consistent with any dominance bias toward high yield. Interstate correlations of G values of the ten lines are mostly positive but not very large. This kind of analysis is apparently of some worth where such data are available but it would seem that the attack outlined in the preceding paragraph would be more efficient and also applicable to more data.

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1. Midcob color described by Demerec some years ago is probably due to one of the alleles of the R series. At least the gene responsible for it shows close linkage with G on chromosome 10. Color in the cob is associated with colored internodes in the stalk.

2. In various strains of the Guarany corn of Paraguay mid-cob color is frequently associated with a faint purple color on the pistillate glumes or bracts. The gene responsible for this color is an allele of P_1 and shows linkage with Y on chromosome 6. In the presence of B the purple glume color becomes very intense and is also extended to the leaves and stalks. This new allele, or another in the series, seems also in certain stocks to be responsible for the basal glume in the tassel.

3. Most of our time and space this season was devoted to determining on which chromosomes are located the multiple-factor segments which distinguish maize and teosinte. Relatively isogenic stocks, homozygous for one or more multiple-factor segments, were produced by crossing four varieties of teosinte with an inbred strain, backcrossing three times to the same inbred, and selfing. These were then crossed to a nine-gene linkage tester and backcrossed to a second nine-gene tester. The ears in these populations were then classified with respect to presence or absence of the multiple-factor segments from teosinte. Such classifications are far from completely accurate, because the effect of the segments vary with the influence of several genes in the tester stock, especially j and g . Linkages can be detected, however, even when the classification is purely arbitrary, although exact crossing-over percentages cannot be determined from these particular studies. The results of these tests are shown in the accompanying table. Analysis of the data was greatly simplified by the use of McBee punched cards which can be sorted with a simple, inexpensive tumbler.

Table I. Summary of linkage relations of the multiple-factor
segments derived from four varieties of teosinte

Variety of teosinte	Number of segments	Linkage with chromosome number									Total number chromosomes tested
		<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>6</u>	<u>7</u>	<u>8</u>	<u>9</u>	<u>10</u>	
Florida	1	-	-	+	-	-	-	-	-	-	1134
"	1	-	-	+	-	-	-	-	-	-	1530
"	1	-	-	-	+	-	-	-	-	-	1575
"	1	-	-	-	+	-	-	-	-	-	1512
"	2	-	-	+	-	-	-	-	+	-	1512
"	2	-	-	+	+	-	-	-	-	-	828
"	2	-	-	I	+	-	-	-	-	-	1386
"	2	+	-	-	+	-	-	-	-	-	675
Summary	12	+	-	+	+	-	-	-	+	-	10152
Durango	1+	-	-	I	+	-	-	-	-	-	567
"	1+	I	-	-	+	-	-	-	I	-	756
"	2	+	I	+	-	-	-	-	-	-	1305
"	3	-	-	-	+	-	-	-	+	-	1494
Summary	7	+	-	+	+	-	-	-	+	-	4122
New	1	-	-	-	-	-	I	-	I	-	1539
"	1+	I	-	-	+	-	-	-	-	-	855
"	2	I	-	-	+	-	I	-	-	-	1575
"	2	-	-	-	+	-	-	-	I	-	1440
Summary	6	I	-	-	+	-	I	-	I	-	5409
Nobogame	1	-	-	-	+	-	-	-	-	-	1359
"	1	-	-	-	+	-	-	-	-	-	765
"	2	-	-	-	+	-	-	-	I	-	1521
"	2	-	-	+	+	-	-	-	-	-	1602
Summary	6	-	-	+	+	-	-	-	I	-	5247
Grand Summary	31	+	-	+	+	-	I	-	+	-	24930

+ = Linkage

I = Indication of linkage

- = Independent inheritance

The important fact gained from this study is that the multiple-factor segments which distinguish maize and teosinte are located on chromosomes 1, 3, 4, and 9 in Florida and Durango teosintes. In Nobogame teosinte which had previously been shown to carry only three major segments, chromosomes 3, 4, and 9 are involved. In "New" teosinte chromosomes 3, 4, 9, and possibly 7 are involved. The remaining chromosomes appear to carry none of the major multiple-factor segments which distinguish maize and teosinte. They are probably not lacking in genes which effect the various characters which distinguish the two species but these are either modifiers or segments too small to be detected by the methods followed in this experiment which depend wholly upon dominant or partially dominant effects.

It should be noted that chromosome 6 was not represented in the nine-gene linkage tester. Previous studies on crosses of Florida teosinte with a stock including bm₁ on this chromosome gave no indication that it is involved in the four major segments.

The exact location of these segments and their length is yet to be determined. The segment on chromosome 1 shows very weak linkage with bm₂ and since previous experiments with Florida teosinte had shown one of the segments to be strongly linked with P at the opposite end it is probable that this segment involves part of the short arm of chromosome 1. There is some crossing over within the segment.

The segment on chromosome 3 shows 25-30 per cent of crossing over with A. This segment is usually transmitted intact. Crossing over, if it occurs at all, is not readily detectable.

The segment on chromosome 4 includes the Su locus. There is considerable crossing over (about 30 per cent) within the segment.

Nothing is known about the position of the segment on chromosome 9, or the amount of crossing over which occurs within it.

The effects of the different segments are alike but not identical. All reduce the size of the seeds, and the diameter of the ear. All of them increase the prominence of the glumes and the number of ears produced on a single plant. At least two of these segments contribute very noticeably toward the reduction of number of rows of grain. In another experiment single segments were first rendered heterozygous by crossing with the original inbred strain, and the hybrid was then crossed with a second inbred to produce a vigorous and uniform F₁ in which approximately half of the plants were heterozygous for the segment. Ears from plants heterozygous for the segments average two rows of grain less than those which lacked the segments.

The segments have no discernible effect upon the pairing of spikelets or response to length of day. It is probable that they carry genes affecting these characteristics but that threshold limitations prevent single spikes from appearing at these levels.

The corresponding segments derived from different varieties of teosinte are similar in the nature and magnitude of their effects. In each case the segment on chromosome 4 is the most "potent." In each case this segment exhibits crossing over within the segment. Furthermore,

a stock derived from Florida teosinte and homozygous for the segment on chromosome 4 is almost identical with a corresponding stock derived from Nobogame teosinte. Differences in teosinte varieties are attributable to: (1) Differences in the number of major segments; (2) the genetic nature of the maize varieties into which they have become incorporated; and (3) the probable presence of additional smaller segments or modifying factors.

We have some evidence that a single segment in heterozygous condition can increase yields appreciably, the extent to which this happens depending in part at least upon the kind of germ plasm with which it is combined. Hybrids involving some inbred strains are noticeably improved when small amounts of teosinte germ plasm are included.

It has so far been impossible to detect these segments cytologically. Stocks heterozygous for the segment on chromosome 4 occasionally exhibit a region of weak pairing on chromosome 4, but since similar regions are found on other chromosomes little significance can be attached to this. Apparently the segments are at least partly homologous to the corresponding regions of maize chromosomes so that there is no regular and distinct failure of pairing.

The new data seem to establish beyond any reasonable doubt the hybrid nature of teosinte. At least the varieties so far studied are nothing more than maize which has been contaminated by another species. The contamination is not a random one but involves multiple-factor segments of four, or in the case of Nobogame teosinte, three chromosomes. These foreign genes must have come either from *Tripsacum*, or from a "pure" variety of teosinte now extinct or yet to be discovered.

P. C. Mangelsdorf

(Ed. note: In correspondence Dr. Mangelsdorf has written, "I have an abundance of seeds of several nine-gene multiple testers and shall be glad to share it with anyone who wants some.")

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"Scattergrain" white double crosses.

In the fall of 1945 a number of farmers' fields of hybrid corn were reported in Kentucky, Tennessee and Indiana which failed to set seed properly. In several fields examined near Henderson, Kentucky, the seed set ranged from as low as about 20 per cent to 85 per cent or better. The difficulty received considerable local publicity and the hybrids concerned were locally designated as "scattergrain" hybrids. The trouble was restricted to white hybrids but the reports indicated that hybrids from several different seed corn companies were involved. Evidence

pointed to male sterility on a field-wide scale as the cause of the poor seed set. The amount of sterility occurring in the same hybrid varied from field to field and seemed to be worse in bottom-land fields that were planted late.

On the basis of information obtained on the pedigrees of some of the offending hybrids, seed of a series of reciprocal single crosses was collected or produced in the greenhouse during the winter of 1945-'46. Observational plantings of these singles and several of the "scattergrain" double crosses were made at Lexington, Berea and Henderson, Kentucky, and at Beltsville, Maryland, in 1946. The data obtained do not permit a critical analysis of the cause of the sterility as, for some unexplained reason, the sterility occurred with a much lower frequency in the single crosses than in the double crosses. Sufficient data were obtained on the sterility, however, to suggest the following as important contributory factors:

1. The sterility seems to occur only in crosses which have a cytoplasmic contribution from 33-16, an old inbred line developed in Indiana.
2. Sterility in the hybrids also is influenced by contributions from the male parent. The substitution of only one line in the male parentage of one of the "scattergrain" double crosses, completely eliminated the sterility in the resulting double cross.
3. The expression of the sterility is very subject to environmental influence.

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Inflorescence structure and row number.

Two abnormalities have previously been described which affect row number in maize, each in its own particular way. (1) Multiplication, recently described by Cutler, produces two spikelets where normally there would be one. In its lowest expression it is responsible for the occasional kernel squeezed in between the regular rows of northern eight- and ten-rowed flints. In its most extreme development it produces the crowded and apparently rowless ears commonly seen in parts of Central and South America. (2) Condensation (Anderson, Ann. Mo. Bot. Gard.) is a telescoping of successive internodes and is most easily analyzed in the tassel. In its extreme form it produces an elliptical or flattened, more or less fasciated ear. In its less extreme expressions it is responsible for most row numbers of 16 or above.

While these phenomena are not unknown in other grasses, as has been demonstrated by Cutler, they are both of them of a more or less teratological nature and it seemed probable that a study of the inflorescence structure in varieties of maize which have neither condensation nor multiplication might be illuminating. A special effort has been made to study such strains and, as anticipated, the structure of their inflorescences (tassels and ears) is much simpler than in other kinds of corn. Particularly as it concerns the central spike of the tassel, it does not seem to have been previously described. It is not spiral but whorled. There are two extreme types, those with whorls of two and those with whorls of three.

Old-fashioned eight-rowed flint corns are an example of one extreme. Their central spikes are in whorls of two pairs of spikelets, each whorl bearing its spikelets at right angles to the whorls immediately above or immediately below. The uppermost tassel branches are also clearly in whorls of two. The other extreme type is found in certain persistently 12- and 14-rowed strains of corn from South America and the Southwest. They have a structure similar to the eight-rowed flints but the central spike has whorls of three pairs of spikelets and the upper portion of the tassel has whorls of three branches. In the Great Plains there are varieties with from 10 to 14 rows. When they are without condensation they show various mixtures of two-whorled and three-whorled.

The apparent spiraling of the central spike is due to the regular alternation of two patterns of spikelet position from node to node. In the eight-rowed flints, for instance, if the spikelets are on the north and south sides at one node they are on the east and west at the next; then the north and south again, and so on. In the 12-rowed corns there is a similar alternation from positions A, C, E, to positions B, D, F, and then back again to A, C, E, producing a six-ranked spike. Since each spikelet pair on the ear produces two kernels of corn the ear-equivalent of a four-ranked spike will be an eight-rowed ear; for a six-ranked spike it will be a 12-rowed ear. The structure of the tassel in these eight- and 12-rowed races is almost transparently simple. The addition of a little condensation or multiplication, however, produces an organ so difficult to analyze that until these less complicated types had been studied the basic whorling was pretty completely concealed.

These observations allow us to put forward a series of hypotheses as to the various processes affecting row number in North American corn. They have already been tested genetically in part; further experiments are under way. The hypotheses are as follows:

There are at least four quite different characters which affect row number in maize. Each operates a different lever so to speak. (1) Maize is fundamentally either in whorls of two branches or whorls of three, or in various mixtures between these two extremes. There are indications that the genetic differences between the two-whorled and the three-whorled are multiple factorial.

In North America this basically simple difference is complicated by the almost universal presence of (2) Condensation. Preliminary genetic results suggest that this may be a single recessive gene, with a number

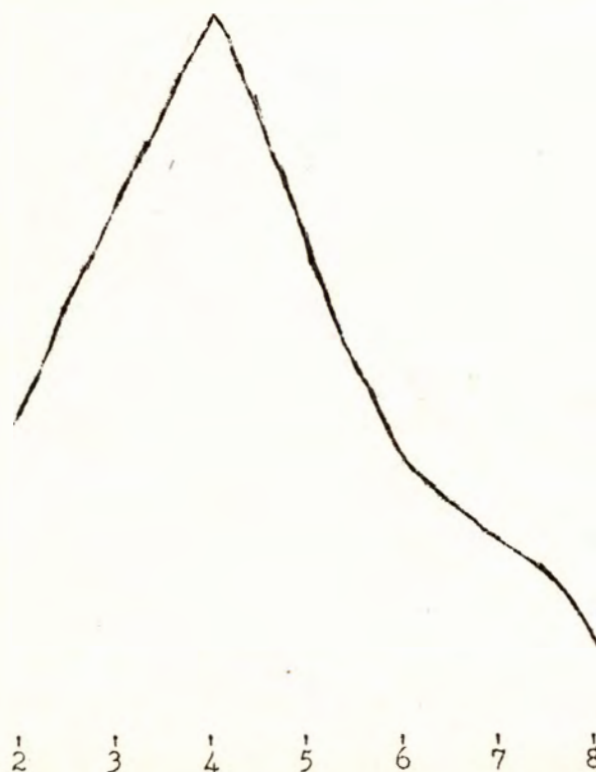
of modifying factors which usually hold down the expression of this fundamentally teratological condition. In Central and South America (3) Multiplication is also an important factor in differences in row number. Nothing is yet known about its inheritance but various states of the phenomenon are known from very slight to very extreme. Except in an occasional inbred it is of little consequence north of Mexico. In addition to the above processes, row number can also be affected by the development or lack of development of the second floret as in Country Gentleman sweet corn and in various strains from South America.

These hypotheses can all be tested by orthodox genetic methods as soon as there are available multiple marker stocks which exhibit extreme values for the above phenomena, viz., condensation vs. non-condensation, three-whorl vs. two-whorl, multiplication vs. no multiplication.

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Among 80 dent corn inbreds of commercial importance, chromosome knob numbers range from 2 to 8 with a frequency distribution as follows:



The modal knob number is 4 with 3 and 5 as the two next most frequent classes. Knob number is strongly associated with at least two

morphological characters - number of rows of kernels and development of husk leaf blades (flag leaves). As knob numbers decrease, row numbers decrease and flag leaves become more pronounced. It is assumed that low knob numbers, low row numbers and long flag leaves were introduced into Corn Belt dent corn from Northern flint varieties. It is interesting and perhaps significant that these characters are so strongly linked that even after a century of breeding they still remain together in dent corn inbreds.

Although exceptions have been observed, there is also an overall correlation between high knob number and shape of ear. For example, those inbreds which approach Mexican Pyramidal in ear shape usually fall into the higher chromosome knob groups.

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New alleles of \underline{A} .

The alleles \underline{A}^b and \underline{a}^P , originating from Ecuador and Peru, respectively, are associated with brown, P-determined, pericarp color (Emerson and Anderson, Genetics 17:503-509. 1932). Both alleles are dominant to \underline{A} (North American origin), which is associated with red pericarp color. Several mutants having intermediate plant color effects and arising spontaneously from \underline{A}^b have a brown pericarp effect which likewise is dominant to the red of \underline{A} (Stadler, News Letter 17:20-21. 1943). The divergent action of the \underline{A} alleles of North and South American origin is revealed further in a series of dosage and dominance studies conducted by the author (Microfilm Abstracts 7: No. 1) and is being investigated further using exotic material collected from isolated regions of Peru and kindly supplied by the Pioneer Hi-Bred Corn Company, Johnston, Iowa. Some results of the preliminary work are reported here.

1. Dominance effects of Peruvian alleles associated with full purple-aleurone color ($\underline{A-P}$). Small progenies from individual, open-pollinated, Peruvian ears were planted at Columbia, Missouri, in 1945 and crosses were made on \underline{aa} and on $\underline{A-}$. The progenies of the \underline{A} crosses with those Peruvian plants which were shown to be homozygous for alleles determining full-purple aleurone color were planted at Ames, Iowa, in 1946. Since the $\underline{A-}$ plants in the 1945 crosses were either \underline{AA} or \underline{Aa} , two kinds of progenies were expected; designating the $\underline{A-P}$ alleles carried by any individual Peruvian plant as $\underline{A-P}_1$ and $\underline{A-P}_2$ these progenies were expected to contain plants of the following genetic constitutions:

Cross (1945)	Types in progeny (1946)			
$\underline{A/A} \times \underline{A-P}_1/\underline{A-P}_2$	$\underline{A/A-P}_1$;	$\underline{A/A-P}_2$		
$\underline{A/a} \times \underline{A-P}_1/\underline{A-P}_2$	$\underline{A/A-P}_1$;	$\underline{A/A-P}_2$;	$\underline{a/A-P}_1$;	$\underline{a/A-P}_2$

Both types of progeny afford a test of the dominance effects of the

Peruvian alleles, the first in compounds with the A allele and the second in heterozygotes with both the A and a alleles. Crosses were made on individual plants within progenies using aa Dt Dt plants as a pollen source. Progeny type was thus distinguished by the presence or absence of dots and this was also the basis for distinguishing A/A-P from a/A-P plants within progenies of the second type. Seven such progenies representing the test of A-P alleles of separate origins in Peru were classified for pericarp color; the available data are summarized in the following tables.

Family	Cross	<u>A/A</u> - P	
		red	brown
117	<u>A/a</u> x <u>A-P/A-P</u>	4	7
119	Same	9	14
120	Same	20	0

Family	Cross	<u>A/A</u> - P		<u>a/A</u> - P	
		red	brown	red	brown
118	<u>A/a</u> x <u>A-P/A-P</u>	3	4	2	3
122	Same	4	5	2	1
123	Same	0	3	0	3
124	Same	5	0	2	0

In spite of the small numbers involved in these progenies it is obvious that the A-P alleles of isolated origin are not similar in their effects on pericarp color. Moreover, in the cases of four of the seven progenies (all excepting families 120, 123, and 124) the two A-P alleles associated in individual Peruvian plants show contrasted behavior. The data suggest that A-P alleles, so far as these progenies represent them, are of two types: One determining red pericarp color and indistinguishable from A; the other determining brown pericarp color and having an effect completely dominant to that of A. There is no evidence for the existence of an A-P allele having a brown pericarp effect which is recessive to A, unless it be found that the progenies of the red pericarp types in families 117, 119 and 120 segregate ears showing brown pericarp color.

2. Dominance effects and response to Dt among Peruvian mutants of the aP and a type. Some of the Peruvian plants which were crossed to A tester in 1945 were not homozygous A-P; six of the test cross ears gave 50:50 ratios for purple; colorless aleurone and two gave 50:50 ratios for purple; pale aleurone. In each of these eight cases some of the seeds having colorless or pale aleurone showed dots. Since the tester parent was adt adt RR CC DtDt in constitution, the presence of these dots establishes with certainty that the colorless and pale seeds are due to mutant alleles at the A locus; if a dominant dilution factor or a recessive factor other than a were responsible for the dilution effects the

seeds would be expected to be without dots. This apparently is the first report of the occurrence of recessive a in South American material; since five of the six Peruvian plants which were found to be heterozygous for a were of separate origin this mutant probably is widely distributed in Peruvian material. It is likely that these types failed to be recognized earlier because of the frequent occurrence in Peruvian material of the recessive forms of the genes R and C, which complement A in pigment production and because they may not have been studied in backgrounds providing the Dt gene which is specific for a.

The action of the pale mutants (designated a^P-P) was studied further in progenies providing the combinations a^P-P/a and a^P-P/A. In the cases of both pale mutants, the combinations with recessive a were invariably associated with brown pericarp color, as were those with A. To test the response of the a^P-P alleles to the Dt gene, crosses were made between a^P-P/a and the tester a^{dl} a^{dl} Dt Dt (the a^{dl} gene does not mutate under influence of Dt). Without exception, the pale seeds (a^P-P/a^{dl}, Dt) on ears from these crosses were without dots, whereas colorless seeds (a/a^{dl}, Dt) on the same ear were dotted. Hence, both a^P-P alleles are similar to a^P in their pericarp color effects and response to Dt, though they may differ from each other and from a^P in the matter of their determination of plant and aleurone pigmentation.

Similar studies are in progress with the six Peruvian a mutants (designated a-P). The limited data which are available at the time point to a divergence in type of action within the a-P group as well as between members of that group and recessive a. All six members are associated with brown pericarp color as determined in heterozygotes with a. Dominance effects in compounds with A have been determined for only two of the six mutants but in both cases there is complete dominance over the red effect of A. This is the first knowledge of an a allele which is associated with colorless aleurone and brown plant color, in which respects it is recessive to A, and yet shows complete dominance to A in its effect on pericarp color. Of the four a-P mutants tested for response to the Dt gene, one proved to be dotted, the other three being without response. The two mutants mentioned as showing dominance to A in pericarp color effect do not respond to Dt. Except for the products of X-ray and ultraviolet treatment there are no past reports of a mutants which fail to respond to Dt; Rhoades (News Letter 15: 6. 1941) describes an a mutant which is indistinguishable from a with the exception that it shows much reduced response to Dt, but this allele, unlike the a-P alleles, is recessive to A in pericarp color effect. The lack of response to Dt reported here for three naturally occurring a-P mutants suggests that the failure to dot in the presence of Dt is not a valid criterion of deficiency at the A locus.

The evidence reviewed here adds to an already complex picture of gene action at this locus. Most significant, from this standpoint, is the evidence on the extreme antimorphism of at least two of the a-P alleles. The antimorphic effects of certain of the A alleles have been reviewed previously (Microfilm Abstracts 7: No. 1). The evidence is not in support of certain hypotheses, notably those of Wright and Stern, which have been advanced to explain antimorphic effects. It is suggested that the antimorphic behavior of the alleles of A may be explained on the basis of an hypothesis which holds a single gene capable of entering into

two different reactions. It is the purpose of further investigation of the Peruvian alleles reported on above to provide additional tests of this hypothesis.

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For a few years observations have indicated that teosinte has more tolerance to heat and drought and possibly more resistance to certain diseases and insect damage than corn. Efforts to improve inbred lines of corn by modifying them with teosinte characters have progressed far enough to give a suggestion of the results to be expected. Various Texas lines were crossed with Florida teosinte, backcrossed to corn from once to three times, and selfed each generation afterwards. In the development of the modified lines, no effort was made to select by observation among the segregates available for use. Plants were selfed at random, and only those plants or ears that were seriously affected with such abnormalities as disease, insect damage, and sterility were later discarded.

Tests of the desirability of the modified lines as compared to the original (unmodified) corn lines were of two kinds: (1) Tests of the lines themselves to compare their tolerance to artificially applied heat; (2) Yield tests of the various lines crossed to a common tester, conducted under field conditions.

1. Heat-tolerance tests. The procedures followed in making tests for tolerance to heat were based on those used for several years at the Kansas Agricultural Experiment Station, although in some respects there are considerable differences between the Kansas methods and mine. Inbred plants of Tx/R-3 and of eight modifications of it were grown and given artificial heat treatments in an oven in six replications, each replication being grown and treated at a different time. Glazed pots with top inside measurement of four inches were used. The pots were selected for uniformity. The soil used for the first five replications was a thorough mixture of sandy loam and compost. That used for the sixth was relatively homogeneous Houston Black Clay.

In each replication, five pots of each line were planted, and an effort was made to have a final stand of two plants to the pot. This procedure usually resulted in 10 plants of each line for each replication.

The plants were given the artificial heat treatment when 13 to 15 days old. The oven used was electric, automatically controlled, with forced ventilation. It was designed for other purposes, and the fluctuation in the temperatures obtained led to some difficulties. However, after a few replications had been treated for practice, the method was found to be usable.

Prior to each application of heat, the soil in the pots was

well-saturated with water. The pots were randomized in the oven and kept under heat treatment for eight hours at 55° C. After the treatment was complete, the plants were kept in the greenhouse for 5 to 30 days without water while the readings of the results were taken. It was found most practicable to take the first reading about 24 hours after treatment, because the extent of the damage to the plants was more readily determined after this lapse of time. The best method found of recording the results was to tabulate the number of days that each plant lived after treatment. In most of the replications no plants were living 10 days after treatment, and those which did live this long or longer were considered not to have been killed by the treatment.

For the purpose of analyzing and studying the results, it was found desirable to assemble all the data for each entry into a single score. In order to accomplish this objective, the combined number of days that all the plants of an entry lived after treatment was adopted as the score. Thus, in the fifth replication of modified line No. 1, the 10 plants lived the following numbers of days: 3, 6, 3, 20, 3, 17, 3, 3, 5, 15. But, since a plant is not considered to have been killed by the heat treatment when it lived 10 days or longer, all numbers above 10 were reduced to 10, and therefore the numbers actually added in order to get the score of this entry were 3, 6, 3, 10, 3, 10, 3, 3, 5, and 10. The score of this entry, therefore, is 56. The highest possible score is 100, and the lowest is zero. The score of each entry is shown in table I, the various lines being listed in descending order of their observed tolerance to heat:

Table I.

Lines	Replications						Average
	1	2	3	4	5	6	
3	45	38	20	85	100	62	58.3
9	32	26	30	100	96	60	57.3
5	47	22	12	90	96	30	49.5
6	28	22	16	71	100	59	49.3
4	26	22	16	60	94	61	46.5
Tx/R-3	36	13	10	50	87	42	40.5
1	22	32	26	77	56	26	39.8
2	18	14	20	30	93	33	34.7
7	36	14	16	34	69	30	33.2

For significance, .05 = 14.6

Since the difference necessary for significance on the .05 level is 14.6, the indication is that two of the lines modified with

teosinte characters are more tolerant to heat than the original line Tx4R-3. Whether tolerance to heat and to drought are related phenomena, as reported by some investigators, has not been determined in this study. However, the yield tests, to be discussed in the following paragraphs, were conducted with that possibility in mind.

2. Yield tests. One yield test was conducted each year from 1943 to 1946 on hybrids involving the group of Tx4R-3 lines tested for heat tolerance, and several tests were conducted on certain other groups. In all the yield tests, the uniform tester was a single cross, commonly one with which the original inbred is combined when put into agricultural use. One or more checks were always included. Except where the contrary is indicated, one check was the original inbred crossed with the uniform tester, and various hybrids whose usual performance was known were often used as supplements.

The most satisfactory results of yield tests were obtained with groups of lines other than Tx4R-3 and its modifications. Although results of the heat tests indicate that additional tolerance has been introduced into Tx4R-3 by crossing it with teosinte, no field test has shown convincingly that the yielding ability of any of the modified Tx4R-3 lines should be adjudged superior to that of the original. Tests conducted during 1945 and 1946 showed only that some of the modified lines were in the same class with the original Tx4R-3 and that others were inferior. As would be expected, one or more modified lines gave actual yields greater than the original Tx4R-3 in each test conducted, but in none of these instances was the difference significant. It should be pointed out, however, that tolerance to drought did not have a fair chance to manifest itself in terms of yield in any test conducted on the Tx4R-3 group. In 1943 and 1944 the yield tests were a failure, principally because of poor stands and accidental damage. In 1945 and 1946 there was no appreciable drought during the critical part of the season.

More interesting results of yield tests were obtained with a group of modified Tx127C lines. A small portion of the results of the two tests conducted in 1945 and 1946 is shown in table II.

The 1945 test of the Tx127C lines contained 36 entries and the 1946 test contained 25 entries. Since the two tests did not contain the same entries, but had only certain ones in common, it is impracticable here to combine all the results briefly in one table. However, the following table does include the highest-yielding entry and one check in each test. The lowest-yielding entry tabulated here from the 1945 test stood 14th among the 36 in the test, and the lowest shown from the 1946 test stood 16th among the 25 in the test. A blank indicates the omission of the entry from the test.

Table II.

Pedigree*	Average yield bu. per acre	
	1945	1946
42116-21-2	44.8	59.5
42116-25-3	42.6	
Tx. Hybrid No. 18 (Ck.)	40.8	
42116-15-2	39.4	65.7
42116-27-1	38.2	49.3
42116-28-5	37.0	55.4
42116-28-4		45.6
Txl27C (Ck.)		44.0
Difference for significance, .05	7.26	9.75
Difference for significance, .01	9.63	12.06

*The tester in each instance was Txl73D x Tx203

It may be observed from these results that some of the Txl27C modified lines, such as 42116-21-2 and 42116-15-2, show considerable promise. It is interesting that some of them gave improved yields during a season when there was no serious drought or other hazard to which teosinte is known to be especially tolerant. Of course there are possible explanations. It seems fairly probable that the introduction of teosinte germ plasm into Txl27C resulted in modified lines with more remote relationship to the tester. Remoteness of relationship between the two parents of a cross is often believed to be an important factor affecting hybrid vigor. Another possible explanation is simply that additional "yield genes" have been acquired from teosinte.

A few teosinte-modified lines of Txl32A and Txl02A have been developed and tested, but the results to the present do not indicate appreciable improvement in them.

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A pair of genes influencing the intensity of yellow endosperm color was reported in the Maize News Letter for January 31, 1944. Segregations of 3 dark yellow to 1 lemon yellow were obtained in selfed progenies. The gene in question was closely linked with opaque-2 in chromosome 7. No symbol was suggested. The situation with regard to the genes for endosperm color is not entirely clear. Five genes have been numbered and one or two additional genes apparently are known. It is suggested that the pair of genes discussed here be designated as $\underline{Y}_8 \underline{Y}_g$.

During the past season data were obtained on a three-point backcross test involving the cross $\frac{+}{\underline{O}_2} \frac{+}{\underline{Y}_8} \frac{+}{\underline{V}_5}$. These data are reported below:

Parental combinations		Recombinations					
		Region 1		Region 2		Region 1 & 2	
404	374	6	11	21	23	0	0
	778		17		44		0
			2.0%		5.2%		0.0

The gene order indicated is $\underline{O}_2 - 2.0\% - \underline{Y}_8 - 5.2\% - \underline{V}_5$.

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Natural teosinte-corn hybrids in Guatemala.

Teosinte occurs as a weed in corn fields over extended areas in the Jutiapa - Progreso - Lake Retana area in south central Guatemala and in the San Antonio Huixta area in the northwestern part of the country. Botanists who have visited these areas, including Weatherwax, Kempton and Popenoe, noted the absence of hybrids in the fields where corn and teosinte were growing together and flowering at the same time. This was surprising in view of the fact that the two species were known to hybridize readily under controlled conditions and their hybrids are fully fertile.

The Jutiapa - Progreso - Lake Retana area was visited in

November, 1946, with Dr. I. E. Melhus, Director of the Iowa-Guatemala Tropical Research Center. A thorough search for natural hybrids was made in corn fields containing teosinte as a weed extending for 40 kilometers along the highways in this area. No hybrids were discovered. Extensive collections of corn and teosinte seed were made from these fields and it is planned to grow this seed to determine whether natural crossing occurred during the current season in fields observed to have corn and teosinte of the same stage of maturity growing in juxtaposition.

Subsequently, the San Antonio Huixta region was visited together with Dr. George Semenuik. As a result of an extended search in this area approximately 30 hybrid plants were discovered. With very few exceptions all of these plants apparently were first generation hybrids having typical four-rowed ears. One hybrid plant with eight-rowed ears and one with predominantly two-rowed ears similar to the teosinte parent were found. Open-pollinated seed from these plants was harvested for a study of the progeny.

An unsuccessful attempt to hybridize Guatemalan *Tripsacum* and corn.

Having been successful in obtaining hybrids between diploid and tetraploid forms of corn and *Tripsacum dactyloides* native in the United States, the possibility of obtaining similar hybrids involving corn and *Tripsacum* species which are native in Central America was investigated. *Tripsacum dactyloides* is not known to occur in Latin America. Of the various species which do occur there, all that have been studied have proved to be tetraploids with approximately 72 chromosomes.

Since very special conditions are required to obtain hybrids of diploid *Tripsacum dactyloides* and diploid corn, the possibility seemed very remote that the tetraploid *Tripsacum* of Central America would hybridize with the diploid corns of that region. However, in developing an hypothesis of the origin of modern varieties of cultivated corn based on the assumption that teosinte resulted from the hybridization of *Tripsacum* and corn and that the chromosome knobs and various other important characters of corn came from *Tripsacum* by way of teosinte, Mangelsdorf and Reeves assumed that natural hybridization of *Tripsacum* and corn did occur in Central America. Hypotheses are of little value unless they can be tested. Fortunately, a direct test of this hypothesis, formulated nearly 10 years ago, involved no special difficulties. *Tripsacum* and corn were found to be in flower at the same time in readily accessible areas in the neighborhood of Guatemala City and Antigua at altitudes of approximately 5,000 feet. More than 200 ear shoots of native corn plants from three different fields were carefully pollinated with *Tripsacum* pollen from plants collected in their natural habitat in the same region. In making pollinations by applying a mixture of *Tripsacum* and corn pollen directly to the bases of the corn silks and in culturing the embryos of resulting aborted seeds, the same technique was used that previously had been successful at Ithaca in obtaining a considerable number of *Tripsacum*-corn hybrids. From three to four weeks after pollination each ear was carefully scrutinized for possible hybrid seed, the embryos of seeds suspected of being hybrid were cultured in a sterile nutrient agar and flown directly to Ithaca where their chromosome number was determined from root-tip counts. There were no hybrid seedlings. All had 20 chromosomes.

This test failed to confirm the assumption of Mangelsdorf and Reeves that in the recent past *Tripsacum* and corn hybrids occurred in western Guatemala, subsequently designated by Mangelsdorf and Cameron as the secondary center of origin of cultivated maize. However, it would be desirable to make additional tests employing other species of *Tripsacum* which are found elsewhere in Central America. Also, a careful search should be made for diploid *Tripsacums* throughout Central America.

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Linkage data on several unlinked characters were gathered and analyzed by graduate students.

1. The silky which appeared in the F_2 of a cross between two inbred lines segregated in an F_2 to give a ratio of 15 normal : 1 si and approximately 3:1 in a backcross.

Red collar (base of tassel glumes) vs. green segregated 9:7 in F_2 in one of these cultures. Based on small numbers, si was independent of red collar, sr, and ms (this ms was supposed to be gs but did not show linkage with sr, also the ears were normal). Red collar was also independent of this same ms and sr. This silky shows no linkage with ms₁.

Backcross tests indicated no linkage between Pl and red collar, a result differing from that reported previously (News Letter 18:16-17. 1944 - Pl vs. red collar = 6.6 per cent recombination). This difference is explainable if red collar is due to complementary factors.

Antonio Marino

I. Z. Hasanain

2. Woodworth's vp gives no evidence of linkage with ms₁. To determine the order of Y, pb, and ms; all very closely linked, Y + ms/y pb+ plants were crossed with y pb ms/+. One y + ms and one y pb ms were obtained, suggesting that this is the order of the three genes.

H. A. McLennan

F. H. White

3. One stock from X-ray treatment has 10 chromosome pairs and about 20 per cent of pollen abortion. The sterility shows linkage with factors in chromosome 2: 43.5% with gl₂, 34.6% with B, and 15.5% with v₄.

Preliminary cytological examination reveals bridges with fragments, indicating an inversion is the probable cause of the sterility, and that the centromere is outside the inversion. The ears show normal fertility.

W. A. Russell

4. A survey of the knob numbers (and where possible the positions) in 20 inbred lines used in the breeding program here is being made to determine possible relationships with plant characters and with combining ability. The knob number varies from two to at least eight.

M. V. Vachhani

The dominant white cap (\underline{W}^c) endosperm factor is linked with brittle stalk (\underline{bk}_2) in chromosome 9, the backcross numbers being 135 $\underline{W}^c +$, 67 $\underline{W}^c \underline{bk}$, 65 $\underline{w}^c +$, 143 $\underline{w}^c \underline{bk}$, or 32.2 per cent recombination. With T 8-9a there was 30 per cent recombination ($\underline{W}^c - T\ 8-9a = 18:33:68:25$). Since tests reported previously indicated no linkage with waxy (News Letter 18:16. 1944) the order appears to be $\underline{wx} - \underline{bk}_2 - \underline{W}^c$; or $\underline{wx} - T\ 8-9a - \underline{W}^c$.

A brown midrib character which appeared in a $\underline{sh} \underline{wx} \underline{gl}_{10}$ culture seems to be genetically different from the other three brown midribs, and therefore is \underline{bm}_4 .

Viviparous (\underline{vp}_5) is the same as Woodworth's \underline{vp} as shown by intercrosses. Tests are in progress to determine the linkage group to which \underline{vp}_5 belongs. This will also locate one of the factors for yellow endosperm (unless \underline{vp}_5 itself causes the color effect).

Progress in building large rings (See News Letter 20:16. 1946).

The different rings of six chromosomes produced as the first step in the program were backcrossed to normals; the progeny were grown and examined for pollen sterility. In each case, plants approximately 75 per cent sterile were identified. These should be carrying the crossover which combines the two parental translocations in one gamete. Similarly, backcrosses of the $F_1\ 0\ 10$ from 1-5-6-7 \times 8 \times 4 were grown. It is hoped that the selected ears represent the desired crossovers, but the sterility classes were more difficult to distinguish by the "pocket microscope" method used in the field.

Chromosome disjunction (See News Letter 19:31. 1945).

In plants heterozygous for T 5-6c, the low percentage of crossing over with the chromosome 5 inversion in the translocated chromosome as compared with the amount observed with the inversion in the normal chromosome can now be explained without resorting to "position effect". When Dr. A. H. Sturtevant saw the data, he suggested that the cytological data on crossing over (percentage frequency of the crossover type or "half disjunction" quartet) did not measure crossing over within the inversion in both cases. When we drew the chromosomal diagrams (checked later) they

showed that this was true. When the inversion is in the translocated chromosome, crossovers within the inversion do not give rise to the cytologically recognizable "half-disjunction" quartets; whereas when the inversion is in the normal chromosome these crossovers are recognizable in that manner. In the one case these quartets result only from crossing over between the translocation break (center of the cross) and the new position of the centromere, consequently comparable to that in the stock heterozygous T 5-6c but homozygous for the inversion.

C. R. Burnham

Linkage data calculation (See News Letter 20:18. 1946).

Fisher (Amer. Nat. 80:568-578. 1946) has presented a simple method of scoring linkage data by using maximum likelihood formulas. To make it readily understood, we have illustrated its application to F_2 and F_3 data commonly encountered in plant material (now ready to be submitted for publication). The formulas, for the scores (remainders) of maximum likelihood formulae when $p = \text{one half}$ is substituted (50 per cent recombination), are:

<u>Source of data</u>	<u>Formulas for scores (c) at $p = \text{one half}$ *</u>	<u>Information (i) per F_2 plant or F_3 line at $p = \text{one half}$</u>
Backcross	$2(a - b - c + d)$	4
F_2	$4\left(\frac{a}{9} - \frac{b + c}{3} + d\right)$	16/9
F_3 from Ab F_2 plants	$4/3(k - 2j)$	32/9
F_3 from aB F_2 plants	$4/3(m - 2l)$	32/9
F_3 from AB F_2 plants	$4/9(8e - f - g - h - i)$	128/81
F_3 from doubly heterozygous F_2 plants	$4(h - i)$	16

* Suitable for repulsion,
change signs for coupling.

By substituting the observed values for a, b, c, d, e, etc., the score (c) for each source of data is obtained.

The total amount of information furnished by the data is ni , where n is the number of plants or of F_3 lines and i is the information per plant or line. Fisher shows that c^2/I is distributed as χ^2 . Each such c^2/I value for each source of data, having one degree of freedom, tests the significance of the deviation from 50 per cent recombination. Then $\chi^2 = (Sc)^2/SI$ tests the deviation from 50 per cent for the pooled data with one degree of freedom. The difference $\chi^2 = S\left[\frac{c^2}{I}\right] - \frac{(Sc)^2}{SI}$ tests

heterogeneity, the degrees of freedom being $(N-1)$ where N is the number of sources of data pooled. For this test a value of p sufficiently close to the best estimate of p should be used. The ratio \overline{Sc}/SI provides an estimate of the correction to be applied to $p = 0.5$ to obtain the p value which best fits all the sources of data.

H. H. Kramer

C. R. Burnham

Study and use of trisomics.

1. The frequency of transmission of trisomics without root-tip chromosome counts can be determined by crossing each trisomic with a homozygous translocation involving that chromosome. The trisomic F_1 plants will show low pollen sterility (25-30 per cent) as compared with the 50 per cent shown by their diploid sibs. With experience the difference can be recognized easily even in the field with the "pocket microscope". I have used it satisfactorily for chromosome 6, using T 5-6a.

2. It would also be desirable to make the trisomic analysis usable by those not able to get chromosome numbers counted. At present only plants trisomic for chromosomes 5 and 7 are phenotypically distinguishable in most crosses, but not in all.

Two tertiary trisomic stocks for each chromosome might be established so that between them the entire chromosome in question would be represented in trisomic condition. If the piece of the attached non-homologue which is also trisomic came from chromosome 5 or 7, it might serve to identify the desired tertiary trisomic plants. Since these tertiaries would also differ from primary trisomics by having approximately 15 per cent of pollen abortion while the primaries would be normal, pollen examination could be used as a supplementary check if desired or if the phenotypes were not distinct.

In place of the 10 primary trisomics, 20 tertiary types would be used for a complete test of the 10 chromosome or linkage groups.

For example, the series might be established from $2n + 1$ (No. 1 chromosome trisomic) \times T 1-5; $2n + 1$ (No. 2 chromosome trisomic) \times T 2-5, etc., selecting the translocation in each case in which the break in 5 was near the middle of the chromosome, assuming a plant trisomic for nearly half of 5 would be most likely to be phenotypically distinct. Two tertiaries would be established for each cross. A series with chromosome 7 also might be usable.

C. R. Burnham

Chromosome disjunction.

In discussing with many others the problem of getting lower sterility from large rings, the possibilities of genic control were suggested. On this basis, a planned search for factors affecting chromosome

behavior at meiosis, such as changed chiasma frequency or position, may be needed. Those studying inbred lines for knob number might be on the lookout for such effects at diakinesis and metaphase. Such stocks would be of interest for other problems also.

Since such factors are likely to be recessives, it will be necessary to study selfed lines from X-ray treatment rather than the immediate plants obtained from the use of X-rayed pollen. I wish to acknowledge the assistance of H. A. McKennan, F. H. White, and K. Hanson.

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Effects of the major plant color genes upon kernel weight in maize.

Brink (1934) has demonstrated that maize plants belonging to the anthocyanin series of color types differ significantly in their average production of grain. Comparison of the four anthocyanin types led to the conclusion that purple was much inferior to dilute sun red, while dilute purple and sun red exceeded dilute sun red in average yield per plant. Subsequent unpublished results indicate that there is probably no significant yield difference between sun red and dilute sun red. Two trials in successive seasons in which dilute sun red (A b pl) and triple recessive green (a b pl) were compared, suggest that dilute sun red has a significantly greater yield.

In 1938 and 1939 the writer conducted three additional experiments at Madison, Wisconsin, in an effort to clarify the status of those color types which had given inconsistent results and in order to include the brown class (a B Pl) which had not occurred in earlier trials. A number of ears resulting from the backcross A₁a₁ Bb Plpl x a₁a₁ bb plpl were obtained. Two experiments, the first including 12 backcross families in three randomized replications and the second, with 18 families in two replications, were grown in 1938. A third experiment (12 families, 3 replications) was grown in 1939. The heterozygous A B Pl plants used in backcrossing were not closely related to the a b pl stock and the segregating progenies exhibited considerable hybrid vigor. Five-eighths of the residual heredity in each family was derived from commercial strains of yellow dent corn adapted to Southern Wisconsin conditions.

The plants were classified as to color type and distinctively tagged. No attempt was made to distinguish the a B pl and a b Pl plants from a b pl in the green class. The frequencies of each type within each row were determined; the mature ears from each color group in a row were harvested together. The samples were dried to a uniform moisture content, shelled, and the shelled corn weighed to the nearest ounce.

The mean shelled grain weights per plant for each plant color class in experiments I and III appear in table I.

Table I.

Mean grain weights per plant by color classes

Phenotype	Experiment I (1938)		Experiment III (1939)	
	No. plants	Mean in lbs.	No. plants	Mean in lbs.
<u>A</u> <u>B</u> <u>Pl</u> (purple)**	674	.307(6)	600	.282(6)
<u>A</u> <u>b</u> <u>Pl</u> (dilute purple)	681	.361(3)	641	.323(2)
<u>A</u> <u>B</u> <u>pl</u> (sun red)	694	.355(4)	686	.318(4)
<u>A</u> <u>b</u> <u>pl</u> (dilute sun red)	688	.372(1)	682	.331(1)
<u>a</u> <u>B</u> <u>Pl</u> (brown)**	698	.344(5)	602	.305(5)
<u>a</u> <u>B</u> <u>pl</u> , <u>a</u> <u>b</u> <u>Pl</u> , <u>a</u> <u>b</u> <u>pl</u> (green)	2002	.368(2)	2000	.319(3)
Total	5437		5211	

** Highly significant differences between this and other classes.

The analysis of variance for each of these experiments reveals that the low yield of purple is highly significant in both cases and that brown with a significantly greater yield than purple is significantly below the yields of the remaining four classes. The relative standings of the six color types with respect to mean grain weight are indicated by the numbers in parenthesis in table I. Dilute sun red has the largest mean in each experiment, the value being significantly ($P = .01$) greater than the pooled mean of the green, dilute purple and sun red classes in each case. In a combined analysis of experiments I and III the difference between dilute sun red and sun red is highly significant.

The results from experiment II are consistent with the other two experiments with respect to the purple and brown classes. The differences are again highly significant. The mean of sun red is second highest in the experiment instead of fourth as in I and III. This high value for sun red in experiment II is subject to question, however, for when the analysis is based upon kernels per ear instead of kernels per plant, sun red is fourth highest while the relative standings of the other are but slightly changed. In this experiment, also, sun red contributes disproportionately to the variance. The error term is larger than in the other experiments making it impossible to pool the results of experiment II with the others. A summary of experiment II and the total frequencies of each color type are presented in table II.

Table II.

Mean grain weights per plant by color classes

Phenotype	Experiment II (1938)		Total plants I + II + III
	No. plants	Mean in lbs.	
<u>A B Pl</u> (purple)**	806	.320(6)	2080
<u>A b Pl</u> (dilute purple)	803	.370(3)	2125
<u>A B pl</u> (sun red)	884	.376(2)	2264
<u>A b pl</u> (dilute sun red)	920	.379(1)	2290
<u>a B Pl</u> (brown)**	848	.345(5)	2148
<u>a B pl</u> , <u>a b Pl</u> , <u>a b pl</u> (green)	2555	.367(4)	6558
Total	6816		17,465

** Highly significant differences between this and other classes.

A chi-square test for the correspondence of the observed frequencies of plants in each color class to the expected 1:1:1:1:1:3 back-cross ratio reveals that the frequencies shown in table II have a probability of .01. The largest deviations occur in the purple class which is smaller than expected and the dilute sun red class which is larger than expected. Since these are the classes which have the lowest and highest mean grain weights, respectively, it appears that the same genotypes which influence kernel weights also influence viability. Relatively large negative deviations also occur in dilute purple and brown, while the sun red frequency exceeds the expected. It seems probable that the dominant gene, Pl, has an adverse effect upon viability.

Plants with the purple phenotype carry the three dominant genes A B Pl and are much less productive than those plants in which one or more of these dominant factors is not present. The brown plants which have the genes B and Pl are at a similar but less marked disadvantage. The dominant genes were always present in heterozygous condition. Since the presence of a single gene A is the only known condition which differentiates the purple from the brown type within a given family, it appears likely that this gene acting in conjunction with B and Pl results in a decreased storage of starch in the kernels. In contrast it is found that dilute purple, dilute sun red, sun red, and green, all have higher mean grain weights than brown. In the three anthocyanin color classes A is present, but b, pl, or b pl are homozygous. The heterogeneous green class includes combinations of a with b, pl or both in homozygous condition. Therefore, it may be concluded that the B Pl gene interaction is effective in reducing the mean weight of grain per plant, presumably by affecting starch storage

during development. The gene, A for anthocyanin pigment, in combination with B Pl increases the effect.

The relatively higher yield of dilute sun red in all three experiments is noteworthy because this is the genotype which is virtually universal among North American varieties of dent corn. While the evidence is hardly adequate to demonstrate that this genotype is always superior in grain yielding potentiality, the fact that A b pl yields are probably significantly greater than those of A B pl is suggestive. In sun red as in purple and brown the development of deeply pigmented tissues must immobilize considerable quantities of carbohydrate which might otherwise be stored in the seeds.

The possibility that the results reported are actually caused by other genes, rather closely linked to the three segregating color genes cannot be entirely rejected on the experimental evidence now available. The foregoing conclusions are based upon a rather homogeneous sample of residual heredity tested in a single locality. Until further evidence is available on the point, however, it would be inadvisable to introduce B and Pl as markers in dilute sun red commercial breeding stocks.

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1. Breeding program.

Brazil may not yet be ready for large-scale introduction of hybrid corn and premature widespread use might lead to a loss of valuable genetical and breeding material in the numerous local populations. In view of these considerations, I have tried since 1937 the following program of establishing homogeneous self-propagating populations.

(a) Selection of the initial material which may either consist of plants of local populations or hybrids containing desired characters.

(b) Selfing during three to four generations and elimination of all pedigree lines which contain undesirable characters.

(c) Sib and between-line crosses during about three generations; selecting the most vigorous combinations, eliminating any hybrid showing undesirable characters; and maintaining all families separately (pedigree).

(d) Thus, the final stage is reached after about seven to eight generations and all the selected families are united into one population which is maintained by open pollination and simple mass selection for stock seeds.

Final results have been obtained by this method in establishing new sweet corn varieties: Piracicaba white P678, P18, orange P9, etc. Satisfactory, though only preliminary results have been obtained also with hard orange flint (cateto) and with yellow dent. After having essentially solved the question of producing sweet corn for our climate, we are now concentrating on the hard orange flints.

The theoretical basis of the process "controlled pollination-pedigree-breeding" is easily explained. It consists in producing a population essentially homozygous for all desired characters, such as grain color and texture, ear size and form, plant height and relative position of ear (slightly above the middle of the plant); and heterozygous for the main factors giving vigor. That such a combination of homozygosis and heterozygosis is possible, was proved in indigenous corn which is on the one side very homogeneous for many seed and plant characters, but at the same time extremely susceptible to close inbreeding.

In Piracicaba sweet corn which is a new synthetic variety we have started the routine work of selfing in order to produce ultimately hybrid seeds.

2. Chemical composition of grain.

The following results were obtained in an analyses of a few of our varieties. The analyses were carried out by the chemists of the "Refinacões de Milho Brazil, S.A." in São Paulo.

			Hard Flint		Dent	
			Cateto	Cateto	Dente	Dente
			P-104	P-114	P-111	P-113
Water	(Umidade)	%	12.81	12.93	13.45	13.61
Protein	(Proteína)	%	10.33	8.58	3.84	8.84
Oil	(Oleo)	%	4.20	4.21	3.92	4.52
Sugar	(Açúcar)	%	0.60	0.68	0.83	0.79
Dextrin	(Dextrina)	%	1.58	1.45	2.00	1.80
Starch	(Amido)	%	66.98	68.60	67.71	66.89
Fiber	(Fibra)	%	2.15	2.25	1.95	2.15
Ash	(Cinza)	%	1.35	1.30	1.30	1.40
Total		%	100.00	100.00	100.00	100.00

Sweet Corn Piracicaba

	White	Orange	Horticulture
Umidade	11.48	11.63	11.95
Proteína	11.21	12.61	11.56
Oleo	7.61	6.74	7.99
Açúcar	3.86	3.53	3.21
Dextrina	22.36	22.78	23.63
Amido	38.38	38.01	36.15
Fibra	3.10	2.80	3.25
Cinza	2.00	1.90	2.25
Total	100.00	100.00	100.00

Note: The three samples of sweet corn contain about five to six per cent of soluble starch, included in the total starch content.

The analyses were carried according to "Food Inspection and Analysis" by Albert E. Leach, S.B. Fourth, 4th edition, p. 304.

There is evidently a very pronounced variation in oil and protein content. Piracicaba sweet corn contains twice as much oil (seven per cent) as the flints and dents. The protein content is also rather high: 12 per cent of total weight or 13.5 per cent of dry weight in sweet corn and 10 per cent in total weight or 11.5 per cent of dry weight in one of the hard flints.

We hope to be able to carry out the analyses on a larger scale this year.

3. Resistance against the grain weevil and moth.

A series of observations have shown beyond a doubt that one type of yellow dent (Monte Olimpo P111) is relatively less attacked by these insects. The studies are being continued.

4. Linkage tests.

The collection of linkage tests is now in the hands of Mr. Nelson Kobal, in continuation of the work by Dr. Graner who has left our Department. Some new lines have been incorporated and others are being constructed. We hope to furnish next year a complete list of our stocks. We expect also to be able from now on to furnish limited numbers of segregating ears for class work.

5. Tunicate.

The work on South American Tunicate is practically concluded. There seems to be no essential difference, either genetically or in phenotypic variability, between pod corn from São Paulo, Minas Gerais or Bolivia. There cannot be any doubt, as far as the seed formation in the tassel is concerned, that there is no difference between homozygous and heterozygous pod corn. Thus, there should not exist any difficulty in maintaining homozygous pod corn through the seeds in the tassel, without the necessity of using in addition a tassel seed factor.

6. Collection of indigeneous corn.

The studies on authentic indigeneous corn are being continued and I hope to publish soon the first results, together with Dr. Cutler. There seems now to be little doubt that one may classify to some extent native corn in accordance with the grouping of the Indian tribes. The main bulk of our collection has been furnished by tribes of the Tupi-Guarany group. There is comparatively little difference between the types cultivated by the Emeremhon (north of the smouth of the Amazon), the Cayabi and other tribes (North Mato-Grosso, almost in the middle of Brazil), the Paragayans and the Chiriguanos (Northern Argentina). The predominant types are: Soft large-grained yellow (aleurone color); semi-hard white;

orange, variegated or red pericarp with some tendency towards dent. There are two rather primitive types; the large ears with flexible rachis and half-submerged grains from northern Mato-Grosso (Caiabi and Bororo Indians) and the small grained pointed pop corns of the Tupi-Indians, which contain many "Tripsacoid" characters.

Both the corn cultivated by the Chavantes of Central Brazil and numerous types cultivated by the Caingang of Parana in the South are completely different, without the predominance of yellow and orange types.

No explanation has as yet been found with regards to the hard orange flints called in the Argentine and Uruguay "Colorado" and "Quarantino", and in São Paulo "Cateto". It may be extracted from crosses of soft yellow and pointed pop.

The genetical analysis of the material is being continued. In the color of red or purple (Pr/pr) aleurone as contrasted to colorless, at least three factors are involved, one the dominant inhibitor Ci. There is at least one dominant inhibitor of yellow endosperm in pointed pop. Floury has more often a polyfactorial basis, rather than the simple fl gene. Waxy seems rather common. Nothing as yet can be stated with certainty about the large number of plant, cob and glume colors. Rose or wood-colored husks are due to new alleles of the P-series.

The Mendelian ratios in Paraguay corn are all perfectly normal. In Bororo corn a gametophyte factor in the IX chromosome causes a deficiency or excess of recessives.

7. Cytology and studies on sterility.

The material from the margins of the Amazon River is characterized by a considerable sterility and we hope to decide this year whether it is simply phenotypic or is a cytological complication.

In several lines of indigenous corn the pollen is heteromorphic or dimorphic.

In Cateto the frequency of different types of defective seed is remarkable. Nothing is known as yet about the frequency of B-chromosomes in this material, though we hope to get fuller information next year.

8. Origin of corn.

Since full accounts have been published no details need be given. Accepting the eastern foothills of the Andes from Peru-Acre down to the Chaco as the center of origin, there are evidently two main centers of domestication: The Quechua group in the Andes and the Tupi-Guaranis in the plains. This year new material from outside these regions will be studied; material from Southern Brazil and, in the north, material from Colombia.

9. Relations between corn and teosinte.

Both comparative morphological and genetic studies convinced me that teosinte is an independent genus, different from both *Zea* and *Tripsacum*. A full account is under publication.

The genetical analysis of *Zea-Euchlaena* hybrids continues. The phenotype of the F_1 and the segregation in the F_2 depend to a large extent upon the varieties used in the cross. Corn characters are less dominant in the order: Piracicaba Sweet, Paulista Pod, Paulista Pointed Pop; and teosinte characters are less dominant in the order: Mexican teosinte and Guatemala teosinte.

In the F_2 and subsequent generations many new combinations have appeared and I am trying to stabilize them; especially intermediate types and what may be called new teosinte "varieties". Among the attempted combinations one may be especially interesting: The combination of corn ear characters and the resistance of teosinte against inbreeding.

The photo-thermo-periodicity of *Euchlaena* is rather interesting. Using earliness in flowering as a measure, we may establish generally the following order from the earliest to the latest: Mexican teosinte, F_1 , Corn F_1 , and Guatemala teosinte. However, in the very rainy summer of 1945 and 1946 the order was maintained with one exception. Mexican teosinte and all teosinte-like segregates in F_2 or later generations became as late as Guatemala teosinte or later still, some not flowering at all; while the F_1 hybrids retained their relative position as indicated in the sequence above. The corn-like segregates and the intermediate forms behaved more or less like the F_1 hybrids.

The analysis of individual gene segregations is under way with the intention of determining the intensity of gametophyte and of zygote elimination both of which are considerable.

10. Publications.

Since all of our papers have been published in Journals with a limited distribution, I am including a list as follows:

Published papers.

- 1938 - F. G. Brieger - Problemas de melhoramento do milho. Revista Agr. 13:3-18.
 F. G. Brieger - Híbridos de milho com referência especial à precocidade. Revista Agr. 13:3-13.
 F. G. Brieger e E. A. Graner - Variações quantitativas do milho "Santa Rosa". Revista Agr. 13:3-24.
 F. G. Brieger e E. A. Graner - Análise da precocidade no milho. Revista Agr. 13:3-17.
- 1943 - F. G. Brieger - Origem do milho. Revista Agr. 18:409-418.
 E. A. Graner - Endosperma amarelo do milho. Revista Agr. 18:443-445.
- 1944 - F. G. Brieger - Estudos experimentais sobre a origem do milho. Anais Escola Sup. Agr. "Luiz de Queiroz". 1:226-278.
 E. A. Graner e G. O. Addison - Meiose em *Tripsacum australe* Cutler e Anderson (*T. dactyloides* subsp. *hispidum* Hitchcock). Anais Escola Sup. Agr. "Luiz de Queiroz". 1:213-224.
- 1945 - F. G. Brieger - Estudos genéticos sobre o milho tunicata. Anais Escola Sup. Agr. "Luiz de Queiroz". 2:211-238.

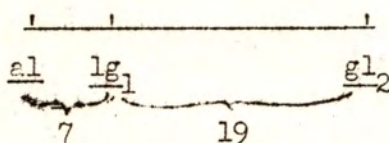
F. G. Brieger - Competição entre Megaspórios em Milho. Anais Escola Sup. Agr. "Luiz de Queiroz". 2:239-267.

F. G. Brieger - Estudos sobre a inflorescência de milho com referência especial aos problemas filogenéticos. Bragantia. 5: 659-716.

H. C. Cutler - Espiguetas de dois grãos no milho. Anais da Escola Sup. Agr. "Luiz de Queiroz". 2:423-430.

F. G. Brieger

1. The al gene (y₃) is seven units from lg₁ in chromosome 2. Its locus in relation to lg₁ and gl₂ is:



2. The y_x gene of Dr. A. M. Brunson, white seeds and albino seedlings (News Letters 18:2-3. 1944 and 20:23-25. 1946) is now called Y₇ and is a new complementary to Y₁ and Y₃. Crosses with y₁ and y₃ gave the following results:

(c) Y₁Y₁Y₃Y₃Y₇y₇Bnbn (X)

Pedigree (1946)	Classes	Seeds	Seedlings obtained		Total of seedlings
			Green	Albion (<u>Y₇</u>)	
11-19 (X)	Yellow-orange	240	231	5	236
	Lemon-yellow (<u>Bn</u>)	101	5	70	75
	White	100	59	25	84
Total		441	295	100	395

(b) (Y₁Y₁Y₃Y₃Y₅Y₅Y₇Y₇Bnbn) (X)

Pedigree (1946)	Classes	Seeds	Seedlings obtained			Total of seedlings
			Green	Albescent (<u>Y₃</u>)	Albino (<u>Y₇</u>)	
153-10 (X)	Yellow-orange	210	192	2	4	198
	Yellow (<u>Y₅</u>)	59	0	51	1	52
	Lemon-yellow(<u>Bn</u>)	75	1	0	69	70
	White	8	0	0	5	5
Total		352	193	53	79	325

Neither cross shows independent segregation for lemon-yellow seeds and albino seedlings. In some strains only the triplex and duplex seeds for lemon-yellow can be separated from the white ones and if this should be the case, the lemon-yellow seeds would give about 50 per cent of green and 50 per cent of albino seedlings (3 green : 4 albino). The \underline{Y}_7 gene shows linkage with the lemon-yellow class. In cross (b) the yellow seeds (\underline{Y}_5) also show linkage with \underline{Y}_7 .

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1. Catalogue of A-B interchanges.

Ten interchanges between A-type and B-type chromosomes have been obtained from pollen treated with X-rays. In the list that follows, the A-chromosome involved in each interchange is indicated by the numeral in the symbol designating the interchange. The A-chromosome in one of the interchanges (TB-A?) is unknown and in another (TB-8?) the identification of chromosome 8 is based on a few rather poor pachytene figures and may be incorrect. The letters S and L refer to the short and long arm, respectively, of the A-chromosome. The distance from the centromere to the point of breakage in the A-chromosome is given as the decimal fraction of the length of the arm in which it occurred.

<u>Interchange</u>	<u>Breakage Point in A-chromosome</u>
TB-1a*	L .2-.3
TB-1b	S .1
TB-4a	S .2
TB-6a	within nucleolar-organizing body
TB-7a	L .9+
TB-7b	L .3
TB-8?	L .3-.4
TB-9a	L .5
TB-9b	S .4±
TB-A?	unknown

*The interchange was originally thought to involve chromosome 2 and was listed as T2-B in Maize News Letter 16: 1942.

The points of breakage in the B-type are as follows: In TB-1a, TB-4a, TB-7a, TB-7b, and TB-8?, they are at or near the junction of the euchromatic and the distal heterochromatic regions. In the others, excluding TB-A? for lack of evidence, the breaks are well within the heterochromatic segment.

2. Behavior of A-B interchanges.

The genetic behavior of TB-1a, TB-1b, TB-4a, TB-7b, and TB-9b

has been investigated in some detail. The results were essentially the same for all five interchanges and can be summarized as follows: The interchange chromosome B^A , which carries the centromere and proximal portion of the B-type and a distal segment of A-chromatin, undergoes non-disjunction in the division of the generative nucleus. The result is that the gametes of a single pollen grain are not alike. One is deficient for the B^A chromosome; the other carries it as a duplication. Both gametes are functional.

When plants that are normal are pollinated with pollen of this kind, two types of seeds are obtained: (1) One has a hyperploid (for B^A) embryo and a deficient endosperm; (2) the other has a deficient embryo and presumably a hyperploid endosperm. If the normal plant used in this cross carries a recessive endosperm gene, the dominant of which is present on the B^A chromosome, the deficient endosperm can be identified by the appearance of the recessive character. Thus, sugary kernels are obtained from the cross, Normal (su su) x TB-4a (Su Su). The hyperploid and deficient embryos have been identified by both cytological and genetical methods.

The interchange chromosome (A^B) carrying the A-centromere shows regular behavior in the division of the generative nucleus. Both interchange chromosomes are transmitted in normal fashion through the eggs.

The rate of non-disjunction, as estimated from the results of crosses involving TB-4a and TB-9b, is very high, approaching 100 per cent. In other words, the B^A chromosome undergoes non-disjunction in the division of nearly every generative nucleus. It seems to be quite regular in behavior in the meiotic divisions and in other mitoses.

3. Genetic location of breakage points.

The location of the point of breakage in the A-chromosome of an A-B interchange may be determined genetically if appropriate recessive testers are used. This has already been illustrated in the case of TB-4a, using the sugary gene. If the corresponding dominant allele is distal to the point of breakage (i.e., in the B^A chromosome), the deficient F_1 progeny will show the recessive character. If it is proximal to this point, the dominant character will appear. The following table gives the results which have been obtained for interchanges tested in this way.

<u>Interchange</u>	<u>Point of Breakage</u>
TB-1a	Proximal to <u>f</u>
TB-4a	Proximal to <u>su</u>
TB-7b	Between <u>v₅</u> and <u>ra</u>
TB-9b	Between <u>sh</u> and <u>wx</u>

4. Evidence of selective fertilization.

A pollen grain in which mitotic non-disjunction has occurred has one gamete lacking a B^A chromosome and another gamete carrying it in two doses. In the double-fertilization process, either gamete may fertilize the egg; the other fuses with the polar nuclei. If fertilization can

occur in either direction at random, we would expect the two types of seeds described in Section 2 to be formed in equal numbers. The frequency of either type would not be expected to exceed 50 per cent of the total progeny, a value corresponding to a rate of non-disjunction of 100 per cent.

In some of the crosses between normal female parents and male parents homozygous for either TB-4a or TB-9b, the percentage of seeds with a deficient endosperm was far in excess of 50 per cent. In the crosses involving TB-9b, a c-tester stock, homozygous for sh and wx as well, was used as the seed parent. The interchange chromosomes comprising TB-9b carried the corresponding dominant alleles. Wx was present in the 9^B chromosome, C and Sh in the B^9 chromosome. The F_1 seeds with an endosperm deficient for B^9 were colorless, shrunken, and starchy.

It was thought, at first, that the excessive number of seeds with a deficient endosperm indicated an outright loss of the B^A chromosome in some of the second microspore mitoses. Suppose that the B^A chromosome lags in this division and is lost to both gametes. Each occurrence of this kind would produce not only a deficient endosperm but also a deficient embryo in the same seed. This result could be distinguished readily from the result of non-disjunction by an examination of the plants obtained from these seeds.

A cytological examination has not yet been accomplished. A genetic test was possible in the crosses involving TB-9b, through the use of scutellum color as an indicator of the presence of C (and therefore B^9) in the embryo. The scutellum is colored when C is present in addition to certain other factors, and is colorless in its absence. Some of the c-tester plants used in these crosses were homozygous for the complementary factors. The F_1 seeds with colorless endosperm were examined for scutellum color and the following results were obtained.

Cross	Colorless endosperm		Colored endosperm	%
	Colored scutellum	Colorless scutellum		
119-11 x 96-8(TB-9b)	227	5	121	66
119-4 x 96-8	95	1	52	66
119-3 x 96-23	129	0	99	57

It is evident from these data that the hypothesis of "outright loss" is untenable as an explanation of the excessive frequency of colorless kernels. The colored scutellum in seeds with a colorless endosperm shows that B^9 is present in the embryo but absent in the endosperm. This would be expected from mitotic non-disjunction. The six exceptional colorless seeds may represent errors in classification since scutellum color varied in intensity and was faint in some embryos. It is also possible that they are due to heterofertilization. The F_1 seeds will be grown this summer for a further check of their constitution with respect to B^9 .

The results so far point to the conclusion that, in some crosses at least, the reciprocal types of double-fertilization do not occur with equal frequency. There is a marked tendency for the hyperploid gamete to fertilize the egg and the deficient gamete of the same pollen grain to fuse with the polar nuclei.

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Effect of the de_{17} allele on seed development.

The de_{17} allele in corn reduces kernel weight to 25 per cent of normal, or less. It shows regular Mendelian transmission. A fair proportion of seeds on the best ears are viable. Once past the seedling stage de_{17} individuals develop into vigorous and fertile plants which, however, are about one foot shorter than their normal sibs. The stock has been propagated in homozygous condition for several generations.

Defective and normal kernels are obtainable at will by pollinating de_{17} plants with de_{17} and De_{17} pollen, respectively. De_{17} kernels develop as well on de_{17} plants as on normals. Defective and normal caryopses increase in weight at the same rate up to nine days after pollination. At 12 days the defective kernels have fallen slightly behind the normals in dry weight. The difference is much larger at 16 days, and continues to increase rapidly up to 24 days beyond which time the defectives make little growth.

Histological studies reveal a relationship between the initial divergence in weight of the two classes of kernels and the differentiation of an absorbing region in the endosperm. Between six and 12 days the cells on the basal surface of the endosperm facing the placental region in normal kernels become elongated, the nuclei move to the inner end of the cells, and the cytoplasm assumes a dense, fibrillar appearance. The basal cells of the endosperm in defective seeds do not become similarly transformed into absorbing elements. Rather, they enlarge about equally in all dimensions and become highly vacuolate. A few days later the cells in this region in defectives begin to break down. Eventually many cells in the basal area and in the adjoining central region of the endosperm collapse and thus become entirely non-functional in the transfer of nutrients to the seed.

The parenchymatous cells of the placenta are quickly and extensively depleted of their total contents by the regularly differentiating normal endosperm. The corresponding cells in kernels possessing defective endosperms are more slowly and less completely depleted. The difference appears to be a direct function of the absorptive capacities of the normal and defective endosperms.

A definite conclusion cannot be reached from the available data whether the de_{17} allele exerts a direct parallel action on endosperm and embryo, or acts directly on the endosperm only. The severely restricted development of the defective endosperm in itself is sufficient to account for the failure of many of the associated embryos to reach a viable condition and for the others to yield weak seedlings. The somewhat shorter stature of adult de_{17} plants, as compared with their normal sibs, may be due either to the handicap incurred at the seedling stage because of poor seed development or to this factor plus a continuing but only mildly deleterious effect of the de_{17} allele on later growth.

R. A. Brink

D. C. Cooper

II. MAIZE PUBLICATIONS -- 1946

(Including certain 1945 publications not previously listed and some early 1947 publications.)

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Maize Newsletter Archives, MaizeGDB, <https://www.maizegdb.org/mnl>; Many *MNLs* available here were retyped from originals; many items, especially of early volumes, are not verbatim, e.g., page numbers and contributors' affiliations are not listed. [Also, some volumes and dates on the website are not consistent with hard copy cover dates.]

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APPENDIX I

Introduction to reprint of Kass, L.B., C. Bonneauil, and E.H. Coe, Jr. 2005. Cornfests, cornfabs and cooperation: The origins and beginnings of the *Maize Genetics Cooperation News Letter*. *Genetics* 169 (April 1): 1787-1797; online May 6, 2005: <http://www.genetics.org/content/169/4/1787.full.pdf+html> [Reprinted with permission of Genetics Society of America].

The following reprinted article provides a perspective on the origins and beginnings of the founding of the Maize Genetics Cooperation and its subsequent *Cooperation News Letter*. It describes how in the early 1920s, the Maize Genetics Cooperation (MGC) began in an informal way among R.A. Emerson and his students at Cornell University. Emerson's ethical and cooperative spirit paved the way for an expanded network of maize researchers who freely shared their materials and unpublished research, thus resulting in rapid progress in fundamental genetic research.

The *Maize Genetics Cooperation News Letter* early volumes reprinted in this book provide documentation for the story told in this historical perspective.

Perspectives

Anecdotal, Historical and Critical Commentaries on Genetics

Edited by James F. Crow and William F. Dove

Cornfests, Cornfabs and Cooperation: The Origins and Beginnings of the Maize Genetics Cooperation News Letter

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IN the early 1920s, the Maize Genetics Cooperation (MGC) began in an informal way among R. A. Emerson and his students. His ethical and cooperative spirit paved the way for an expanded network of maize researchers who freely shared their materials and unpublished research, thus resulting in rapid progress in fundamental genetic research (COE 2001; KASS and BONNEUIL 2004).

The first letter summarizing both published and unpublished maize linkage data was compiled by Emerson and his student George Beadle and sent to students of maize genetics on April 12, 1929. This communication was an outcome of a “cornfab” held in Emerson’s hotel room in December 1928, during the annual American Association for the Advancement of Science (AAAS) meetings. The “Historical Notes on Maize Cooperation” identifies Emerson’s 1929 communication as the *first* Maize Genetics Cooperation News Letter (MNL; EMERSON 1940). Beadle was the first secretary of the MGC and he solicited material for additional summaries of linkage data, which were distributed in two parts in 1930. Rhoades succeeded Beadle as secretary and continued to summarize and publish the reports of cooperators in the MNL, which continues to be published annually.

The cooperators met at the Sixth International Congress of Genetics (ICG) at Ithaca in 1932 and organized a committee to establish the maize stock center at Cornell University and to seek funding for their enterprise. Emerson’s grant application to the National Research Council (NRC) was denied and he was encouraged to apply immediately to the Rockefeller Foundation (RF),

who granted him funds to support his information and supply network in 1934. The work of Barbara McClintock in cooperation with Beadle, Rhoades, Creighton, Burnham, and others at Cornell between 1928 and 1934 resulted in a definitive correlation of chromosomes and linkage groups in maize—ultimately published in 1935 by Emerson *et al.* The cytogenetics of maize was also reviewed in that year (RHOADES and MCCLINTOCK 1935).

The exhibits that Emerson submitted to support his Rockefeller Foundation grant included a historical summary of the MGC and MNL. These documents allowed us to reconstruct the events that established these important resources for the maize genetics community. Emerson’s legacy lives on in the cooperative spirit of maize researchers and in the News Letter he founded 75 years ago.

At the 1932 ICG held in Ithaca, New York, Rollins Adams Emerson (NELSON 1993), Head of the Department of Plant Breeding at Cornell University, gave an opening address titled, “The Present Status of Maize Genetics.” In his introduction he declared, “I cannot refrain from noting here a very real advantage experienced by students of maize genetics . . . I am aware of no other group of investigators who have so freely shared with each other not only their materials but even their unpublished data. The present status of maize genetics, whatever of noteworthy significance it presents, is largely to be credited to this somewhat unique, unselfishly cooperative spirit of the considerable group of students of maize genetics” (EMERSON 1932, p. 141; KASS 2001).

During this Congress, Emerson called a meeting of ~45 students of maize genetics and formalized what would soon be called the Maize Genetics Cooperation. Following their meeting Emerson and his graduate student Marcus Rhoades issued on October 5, 1932, what has long been considered the first Maize Genetics Co-

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FIGURE 1.—R. A. Emerson with former and current students and colleagues at Fernow Hall, Cornell University, January 1, 1922, following the AAAS meeting in Toronto, where the second “cornfest” was held. Back row, from left to right: Milislav Demerec, Sterling Emerson, Ernest G. Anderson, and Charles Metz; front row, from left to right: Maxwell J. Dorsey, Sewall Wright, Rollins A. Emerson, William Bateson, Claude Burton Hutchison, Calvin Bridges, Frank P. Bussell, and Lewis A. Eyster (with permission of Royse P. Murphy, Department of Plant Breeding, Cornell University; see also PROVINE 1986, p. 103).

operation News Letter (RHOADES 1932a). Our research (BONNEUIL and KASS 2001; COE 2001; KASS and BONNEUIL 2004; E. H. COE and L. B. KASS, unpublished results), which we offer in keeping with the long tradition of maize cooperation, provides a historical perspective on the actual origin of the MGC and the beginnings of the MNL, which was first issued in 1929. We present here the history of Emerson’s successful negotiations with the Rockefeller Foundation to fund his cooperative enterprise at Cornell University following his unsuccessful attempt to obtain funding from the NRC. Future Nobel laureates George Beadle, Emerson’s student, and Barbara McClintock, Lester W. Sharp’s student and Beadle’s collaborator, freely submitted their results to the MNL; this laid the groundwork for a similar publication, the *Drosophila Information Service*, for the *Drosophila* geneticists in March 1934 (BRIDGES and DEMEREC 1934) and for the *Worm Breeders Gazette*, the community newsletter of the roundworm biologists (EDGAR 1975; COHEN 1995), among others. We rejoice in the founding of Emerson’s ideal and celebrate the 75th anniversary of the MNL.

EARLY COOPERATION

Cornfests—a cooperative enterprise to map maize:

As early as November 1918, Emerson wrote to Donald F. Jones at the Connecticut Agricultural Experiment Station that he was “hoping that all the men in this country who are working on related problems with corn may cooperate to such an extent that we can cover the field more quickly” [Emerson to Jones, November 8, 1918, Division of Rare and Manuscript Collections, Carl

A. Kroch Library, Cornell University (CU) Library, Ithaca, NY]. Soon afterward, Emerson arranged informal “cornfests” in conjunction with the AAAS meetings. It seems that Emerson organized these ~10 years before the famous “cornfab” held in his hotel room in New York City in December of 1928, as recalled by RHOADES (1984). Emerson much earlier had invited Paul Weatherwax of Indiana University to attend a “second cornfest” along with the “general genetics section” he had planned for the AAAS meetings in Toronto in 1921. Weatherwax apologized for not being able to attend (Weatherwax to Emerson, November 22, 1921, CU) but Emerson’s former and current students and colleagues joined him there and, following the meeting, held a reunion on January 1, 1922, at Cornell (Figure 1).

The following winter, Emerson emphasized the importance of agreeing on uniformity for factor notation (gene symbols) and he set the tone for cooperating on this problem in a letter on March 7, 1923 (EMERSON 1923, p. 147), “To Students of Corn Genetics: . . . It seems wise to follow the notation used by the *Drosophila* workers, tho, in some respects, their usage is perhaps no more nearly consistent than our own.” Emerson also asked his colleagues for assistance with numbering the maize linkage groups and requested advice on using bilateral gene symbols:

Shall priority of publication of any linkage determine the numerical order? Or shall the order be determined arbitrarily? . . . I suggest . . . that we number the groups in the order given by [William H.] Eyster and by [Claude B.] Hutchison as follows: 1-*C-wx*; 2-*g-R*; 3-*su-Tu*; 4-*B-Lg*; 5-*Y-Pl*; 6-*Pf*. . . . It may be wise, however, to assign no numbers to groups other than the six listed above until the newer groups have been tested further. Another prob-



FIGURE 2.—R. A. Emerson and members of the Synopsis Club, 1923. Herbert J. Webber started this student/faculty organization at Cornell in 1907, and Emerson continued and encouraged member participation (Department of Plant Breeding Records, Courtesy of the Division of Rare and Manuscript Collections, Cornell University Library). Members are identified from left to right (an asterisk designates corn researchers). Front row: William T. Craig, J. Randal Livermore, Ernest Dorsey, Franklin D. Keim, Robert D. Lewis, Laurens J. Henning, John P. Jones, *Helen A. Z. Trajkovich, G. V. Wazalwar. Second row: Frank P. Bussell, *Allan C. Fraser, Harry H. Love, *Rollins A. Emerson, Clyde I. Myers, *Roy G. Wiggans, *Lester W. Sharp, *Lowell F. Randolph. Back row: T. Sasaki, Archie F. Barney, Harold D. Brown, Leo A. Van Rooyen, *Pavao Kvakan, Andrew D. Suttle, Walter A. Burkholder, Lua A. Minns, Edward L. Proebsting, Clifford V. Kightlinger, Merl C. Gillis, and *Iang Chandrastitya.

lem is bothering us. Shall we continue to use bi-literal symbols for genes as we have usually done in the past [*i.e.*, *bl*, blotched leaf], or adopt the recommendations of the Naturalist's committee to use single letter symbols [*i.e.*, *b₁*]? If the corn men desire to stick to the use of bi-literal symbols, we shall probably have to refrain from publishing in *Genetics* . . . but if the corn men think best to adopt the plan followed by *Genetics* [using single letter symbols], I shall use it (p. 149).

Emerson ended his five-page review with words for continued cooperation, "I am sending this to a considerable number of corn genetics workers. When I have received replies from the majority, I may want to refer some of our problems to the Chairman of the Naturalist's committee with the suggestion that he consider the advisability of referring it to the committee for consideration" (p. 149).

Two of Emerson's former students at Nebraska, Ernest G. Anderson (Figure 1) and Ernest W. Lindstrom, had followed him to Cornell in 1914 and continued to work on corn problems after graduating. Students and established researchers from around the country and throughout the world soon joined Emerson's group and studied corn breeding and genetics at Cornell. C. B. Hutchison (Figure 1), a former Cornell graduate, was appointed Professor of Plant Breeding in 1916. By 1921, he continued Emerson's unpublished study of *C-Sh* linkage and established that *Sh* was part of the *C-Sh-Wx* linkage group (HUTCHISON 1921, 1922). When Allan C. Fraser (Figures 2 and 3) succeeded Hutchison, he turned (from wheat) to maize (FRASER

1924). In addition to Anderson and Lindstrom, several other students pursued graduate work with Emerson on corn genetics (including women and students from abroad, Figures 2 and 3): William H. Eyster, Milislav Demerec (Figure 1), Helen A. Trajkovich, Pavao Kvakan, Thomas Bregger, Ivan F. Phipps, George W. Beadle, Hsien W. Li, George F. Sprague, Johannes D. J. Hofmeyr, Marcus Rhoades, Swarm Singh, Sylvia Allen, and others (R. P. MURPHY, unpublished results; CU).

During the period 1918–1920, Emerson realized that he could not avoid investigating the linkage of maize, which was crucial both to closing the gap with *Drosophila* workers and to providing a deeper basis for the breeding work on corn. Whereas from 1913 to 1928 *Drosophila* linkage mapping remained the concern of a few laboratories (WAGNER and CROW 2001), Emerson promoted the idea that maize genetic mapping should be a larger cooperative enterprise (KASS and BONNEUIL 2004), which would allow individuals to devote the best of their research time to more fundamental research projects. Furthering this end, Emerson also developed a regular collaboration and acted as advisor to the U.S. Department of Agriculture (USDA) program in corn research from 1920 onward [U.S. National Archives and Records Administration (NARA), College Park, MD]. Several graduate students, including Barbara McClintock, George Beadle, and Marcus Rhoades, were supported at Cornell by USDA funds, and some graduates obtained jobs with the USDA, including Arthur M. Brun-



FIGURE 3.—R. A. Emerson, Mr. S. C. A. R. Crow, and students of corn genetics posing in front of the Plant Breeding shed near the Plant Breeding Garden at Cornell University, 1927 (see also KASS and MURPHY 2003) (courtesy of William B. Provine). From left to right, front row: Hsien W. Li (China), Ivan F. Phipps (Australia), Allan C. Fraser, George Beadle's dog (Toto), George W. Beadle, and Harold B. Riley. From left to right, back row: Thomas Bregger, George F. Sprague, R. A. Emerson, S. C. A. R. Crow, Professor Emerson's dog, Roy G. Wiggins, and Wiggins' technician.

son, Thomas Bregger, Lowell F. Randolph, Marcus Rhoades, and George Sprague, all of whom contributed to the cooperative endeavors.

Following Emerson's early work on multiple factor inheritance (EMERSON and EAST 1913), his maize genetics school contributed concurrently to the progress of corn breeding and to general knowledge in genetics. In this respect, Emerson's program may be considered a parallel to Thomas Hunt Morgan's group [at Columbia University and later at The California Institute of Technology (Caltech)]. Emerson's students had close scientific associations with the *Drosophila* geneticists and with geneticists and cytologists at other institutions. Concepts, methods, standard nomenclatures, along with students (including E. G. Anderson, M. Demerec, G. Beadle, and M. Rhoades) who were trained in corn genetics and later also worked on *Drosophila*, circulated between the two communities. Maize geneticists maintained strong relations with *Drosophila* geneticists during the 1920s (e.g., C. Metz, C. Bridges; Figure 1). This connection was due primarily to Emerson and his students, who kept Emerson informed about the exciting work that was progressing in these laboratories. Consequently, Cornell maize geneticists were aware that the use of cytogenetics by *Drosophila* geneticists had opened a fertile second front to tackle problems.

Linkage groups: By 1928, however, significant general contributions to genetics from corn were quite limited (McCLELLAND 1930). Furthermore, maize linkage studies and genetic mapping stood nearly a decade behind *Drosophila*. The 10 linkage groups in corn were not all clearly identified and the mapping work in each group was still very rough, as illustrated by the "rainbow maps" drawn by Beadle and Emerson in April 1929 (Figure 4) (EMERSON 1929).

Within the year, however, Barbara McClintock's identification of the morphology of the corn chromosomes (MCCLINTOCK 1929) and her unpublished research on

trisomic ratios correlating genes with specific chromosomes were major contributions to Beadle's "Summary of Data on the Independence of the Linkage Groups in Maize," which Emerson distributed "To Students of Maize Genetics" on April 17, 1930 (EMERSON 1930a). McClintock, then an instructor at Cornell, collaborating with students George Beadle, Henry Hill, Harriet Creighton, and Marcus Rhoades, and with Charles Burnham, a visiting scientist, and others, began a golden age for maize genetics and cytogenetics at Cornell (RHOADES 1984).

At the Ithaca Congress in August 1932, Emerson could confidently present a genetic map with linkage groups correlated with numbered chromosomes, thus setting the stage for further cooperative and significant contributions to maize cytogenetics (RHOADES and MCCLINTOCK 1935). Rhoades also organized a "living chromosome map" in which mutant plants were arranged according to their chromosomal positions (CROW 1992).

FOUNDING THE MAIZE GENETICS COOPERATION NEWS LETTER

By February 1934, Emerson had applied to the RF for a grant-in-aid for support of work in collecting and disseminating maize stocks and information (CU). Emerson submitted a separate portfolio of exhibits (RF exhibits A–J, Rockefeller Foundation Archives, Sleepy Hollow, NY) to document his application dated February 6, 1934. Emerson's "Historical summary of cooperation among maize geneticists" (RF exhibit A) described how the maize cooperation began ~15 years previously in a small way among his former students. Soon other investigators were asked to be included. He documented interactions among these researchers with a "mimeographed summary of linkage in maize, 1929 [*sic*]" (RF exhibit D); this exhibit was actually Emerson's "second folder of mimeographed information issued sometime

C sh wx Group

C-SH-WX GROUP		
List of Genes		
ar	Argentia - finely striped leaf	Eyster 1929
au ₁	Aurea chlorophyll-yellow plant	Eyster 1929
au ₂	Aurea chlorophyll-yellow seedling	Eyster 1929
bp	Brown pericarp with a	Meyers 1927
C	Colored aleurone with A and R	East and Hayes 1911
d ₃	Dwarf plant	Suttle (Unpub.)
de ₁₅	Defective endosperm	Brink 1927
fl	Floury endosperm	Hayes and East 1915
gl	Glossy seedling	Hayes and Beowhelen 1925
gm ₁	Germless	Eyster 1929
I	Inhibitor for aleurone color	East and Hayes 1911
pk	Polkadot leaf	Eyster 1929
v ₁	Virescent seedling	Demerec 1924
v ₁₄	Virescent seedling	Phipps (Unpub.)
v ₁₅	Virescent seedling	Phipps (Unpub.)
w ₁₁	White seedling	Demerec 1926
wx	Waxy endosperm	Collins 1909
yg	Yellow-green plant	Jenkins 1927

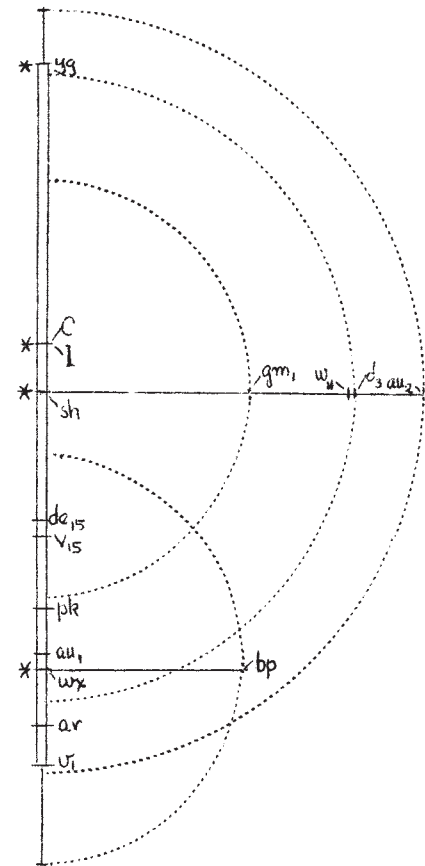


FIGURE 4.—Linkage group 9 and Rainbow map as of April 12, 1929 (after EMERSON 1929; excerpted from E. G. Anderson's annotated copy in MNL archives; reprinted in MNL, Vol. 53, pp. 118–119, 1979).

after the first one" (mentioned in EMERSON 1940). His "mimeographed summary" (RF exhibit D) included all of the linkage data compiled and sent to maize geneticists on April 17, 1930, and July 26, 1930 (EMERSON 1930a,b). Emerson's *first* (our emphasis) mimeographed letter, dated April 12, 1929 (EMERSON 1929), "considered News Letter 1" by Emerson himself (see EMERSON 1940), was distributed to maize geneticists shortly after the "corn-fab" held in Emerson's hotel room at the time of the AAAS Christmas meetings in New York City in 1928. It included a long folder of linkage information and the names of researchers assigned each linkage group (see Table 1 based on the original). Emerson (April 12, 1929) carefully explained, "To those not at the New York Meeting . . . this assignment [of linkage groups] was . . . made in accordance with the expressed interests of those assuming the responsibilities entailed. It was far from our purpose to preempt groups for ourselves and thereby warn off other workers. Our purpose rather was to make sure that each known group would be given immediate and adequate attention to the end that the not very exciting job of chromosome mapping may go forward with some dispatch, thereby making possible an

attack on certain important genetic problems now awaiting just such tools as accurate linkage maps afford" (EMERSON 1929, p. 117).

Although Barbara McClintock's name appears amid Emerson's list of cooperators, we have no documentation that she attended the meeting and it would not have been appropriate in that era for a single woman to attend a gathering in a man's hotel room. The cooperators who did attend, however, were most familiar with McClintock's work (see KASS 2003) and would have recommended her for this endeavor. Following the New York meeting (December 1928), George Beadle acted as secretary of the group (BEADLE 1929a,b, 1930; EMERSON 1931). Beadle requested from maize cooperators the summaries of linkage data, which Emerson, in cooperation with Beadle and Fraser, would send to cooperators in the spring and summer of 1930. Beadle left Cornell in late 1930 for Caltech as a National Research Council Fellow (Plant Breeding Records, CU) (BERG and SINGER 2003), but continued to receive unpublished linkage data from cooperators (EMERSON 1931), until Marcus Rhoades subsequently succeeded him as secretary (RHOADES 1932a).

In his review of "The Early Years of Maize Genetics,"

TABLE 1
To whom linkage groups were parceled out at New York, at the “Cornfab”
held in R. A. Emerson’s hotel room in December 1928

Linkage group	Recipient
C-Wx	Eyster (Bucknell University); Beadle (Cornell University)
R-G	Lindstrom, Jenkins, Wentz (Iowa State University)
Su-Tu	Emerson (Cornell University)
B-Lg	Stadler (University of Missouri); McClintock (Cornell University)
Y-Pl	Hill (Cornell University)
P-Br	Emerson (Cornell University)
Ra-Gl1	Brewbaker (University of Minnesota); Jorgenson (Ohio University); Li (Cornell University)
D1-Pg2	Not assigned
A-Ts4	Brink (University of Wisconsin); Li (Cornell University)

Based on EMERSON (1929).

RHOADES (1984) recalled the New York City “cornfab,” which was his first with the maize cooperators. Rhoades had arrived at Cornell in the fall of 1928 from the University of Michigan, where he had studied with Emerson’s former student E. G. Anderson. Anderson was soon recruited by Morgan for his newly established Biology Division at Caltech. Rhoades then spent the 1929–1930 academic year there with Anderson (CU) (ANDERSON and RHOADES 1931; BIRCHLER *et al.* 2003). It seems clear, however, that the 1928 AAAS “cornfab” was not Emerson’s first.

ESTABLISHING AND FUNDING THE MAIZE
GENETICS COOPERATION AT CORNELL

Establishment of the Maize Genetics Cooperation: Emerson also submitted to the Rockefeller Foundation a copy of Rhoades’ first letter to corn geneticists dated October 5, 1932 (RF exhibit C; RHOADES 1932a), which was retroactively numbered “Vol. 2,” in the Cornell Plant Breeding Department’s bound volumes of the MNL [MNL, Vols. 2–14, 1932–1940, and MNL, Vols. 15–21, 1941–1947; Plant Breeding Department Archives (PB), Cornell University, Ithaca, NY]. Therein, Rhoades summarized the resolutions discussed and favorably acted upon by a committee of maize-genetics workers at the Ithaca meeting held on August 26, 1932, in connection with the International Genetics Congress. In addition to discussing the numbering and naming of gene symbols, linkage groups, and chromosomes, the group agreed that Cornell should be the “clearing house” where the records would be kept and that a repository should be formed for storing and disseminating the new information. Emerson, chair of the committee to oversee their resolutions, along with R. Alexander Brink, Donald F. Jones, Paul C. Mangelsdorf, and Lewis J. Stadler, had chosen Rhoades (1) to act as custodian of the seed stocks, (2) to furnish a list of stocks received, and (3) to distribute stocks to workers. They also reallocated the 10 maize linkage groups to individuals who would

assume primary responsibility for the group assigned (Table 2) (see also Coe 2001).

By this time McClintock had left Cornell but her pioneering contributions to maize cytogenetics had been both recognized and rewarded. She was awarded a National Research Council Fellowship (1931–1933) and, after spending time with L. J. Stadler at the University of Missouri, had joined Anderson’s group at Caltech, where she resumed cooperating with Beadle and Burnham. They returned to Cornell to attend the ICG in the summer of 1932, where EMERSON (1932) recognized their contributions to maize cytogenetics.

Following the Congress, Rhoades’ first letter to maize cooperators made clear that “anyone may begin or continue to work with any group whether or not it has been assigned to him.” It was expected that when “two or more are interested in the same group, they will work in close cooperation!” Rhoades then distributed a call for stocks, wants, and news items, on December 12, 1932 (RHOADES 1932b), and the third Corn News Letter followed on January 23, 1933 (RHOADES 1933; RF exhibit C in part). These two letters are bound together at Cornell (MNL, Vols. 2–14, 1932–1940, PB) and the latter is numbered “Vol. 3.”

Funding the Maize Genetics Cooperation: Emerson’s “historical summary” (RF exhibit A) additionally revealed that his committee was also responsible for devising a way to “carry out the work which the Cornell maize geneticists were asked to continue and to enlarge.” His committee did not find a way to provide funds, but it led to an alternative opportunity. The committee on agronomy appointed by the Division of Biology and Agriculture of the NRC, a unit of the National Academy of Sciences, unanimously recommended a grant-in-aid of \$1000/year for 5 years for an information and supply service for maize work to be headed by R. A. Emerson of the Plant Breeding Department of Cornell University, for the purpose of maintaining the service for “one of the most important crops and . . . for extending our knowledge in the field of genetics and cytogenetics”

TABLE 2
Reassigned linkage groups

Linkage group	Recipient
Group 1, P-br	Emerson
Group 2, B-lg	Beadle
Group 3, a1-Rg	Brink
Group 4, su-Tu	Jones
Group 5, pr-v2	Burnham
Group 6, Y-Pl	Stadler
Group 7, gl1-ra	Jenkins
Group 8, j	Sprague
Group 9, c-wx	Eyster
Group 10, R-gl	Lindstrom

Maize linkage groups 1–10 were reassigned to individuals by the committee of maize researchers convened at the ICG on August 26, 1932 (after RHOADES 1932a). Researchers listed are from Rhoades' letter of October 5, 1932.

(RF exhibit B). The NRC committee supported their recommendation with six exhibits (cited as exhibits I–VI), which Emerson had submitted to document his accomplishments to date. These exhibits were not in the files at RF but we did locate two exhibits identified by Roman numerals: exhibit IV, Rhoades' letter dated December 12, 1932 (RHOADES 1932b), and exhibit V, dated January 23, 1933 (RHOADES 1933); we found these numbered exhibits in archived files of the Maize Coop (see also EMERSON 1940, where maize communications are identified by roman numerals). The committee, composed of M. Francis Morgan, Ralph J. Garber, and Richard Bradfield (chairperson), emphasized that “maize occupies about the same relative position among plants that the fruit fly *D. melanogaster* does among insects” (RF exhibit B). Surprisingly, their recommendation was not accepted by the Council.

On December 26, 1933, the secretary of the NRC committee on grants-in-aid notified Emerson that after careful study of the application they had decided against making the grant of funds. Emerson received their letter upon returning from the Boston AAAS meetings, where both maize and *Drosophila* geneticists had suggested “standardizing nomenclature and symbolization for maize” (RF exhibit H). While there, Emerson had discussed with Frank Blair Hanson (Assistant Director, Natural Sciences, Rockefeller Foundation) an alternative plan for applying for funds to the Rockefeller Foundation should the NRC grant not be approved (Hanson's diary, RF). Four months previously (September 1933) RF officers Warren Weaver (Director, Natural Sciences) and Hanson, while visiting Cornell on other matters, had been apprised of Emerson's “information and supply service to corn geneticists” and his need for funds; but at that time Emerson was confident that the NRC would support the work (Weaver's diary, RF; Emerson to Stadler, November 8, 1933, CU).

Within a month of learning that the NRC grant appli-

cation had been denied, Emerson applied to the Rockefeller Foundation for funding and submitted Rhoades' most recent “mimeographed letter to maize geneticists,” dated January 25, 1934 (RF exhibit J; MNL Vol. 4, PB). By this time, among the 53 maize geneticists engaged in cooperative work on genetic mapping, it appears that not fewer than 30 were Emerson's collaborators at Cornell, had been graduate students there, or had done some postdoctoral work in his department. Emerson identified 24 cooperators as “most actively engaged in genetic studies”; 16 had been graduate students and 2 had been postdoctoral fellows at Cornell (RF exhibit E). He submitted the exhibits (RF exhibits A–J), which we have described here, and also explained that in the spring of 1933, parts of a manuscript of “A Summary of Linkage in Maize” then in the course of preparation by Fraser, Beadle, and himself (RF exhibit F) “together with work sheets had been sent to those to whom particular linkage groups had been assigned.” The draft manuscript was, of course, the notable “A Summary of Linkage Studies in Maize” that would be published by Emerson, Beadle, and Fraser in 1935.

On March 16, 1934, the Rockefeller Foundation appropriated \$5000 for the New York State College of Agriculture at Cornell University for the “support of collecting and disseminating maize stocks and information relating thereto” directed by Professor R. A. Emerson. Within the week, EMERSON (1934) asked cooperators if they were willing to allow him to use their unpublished linkage data in “the much heralded and too long delayed” general linkage summary to be published from Cornell (NARA). Students of maize genetics responded without reservations, fostered by Emerson's cooperative and enthusiastic, yet trustworthy, nature. Emerson soon after announced the Rockefeller award in a letter to cooperators on September 13, 1934 (MNL Vol. 7, 1934, PB). At that time, 60 genetics researchers were receiving the News Letter.

By April 1934, McClintock returned to Cornell where she completed her year-long Guggenheim Fellowship but worried about finding a job (KASS 2003). Emerson recognized her abilities toward his MGC enterprise and requested a separate grant-in-aid to hire her as his research assistant (RF; CU; KASS 2003) for continued research on maize cytogenetics. With Emerson's encouragement, his students took advantage of her presence to learn new techniques and to receive her cooperative guidance. Within the year, EMERSON *et al.* (1935) recognized McClintock's, and other maize cooperator's, contributions toward their maize linkage studies. Their linkage summary reported that, using trisomic ratios, McClintock identified 8 linkage groups with chromosomes 2, 3, 5, 6, 7, 8, 9, and 10. In 1935, Rhoades and McClintock reported that, by using trisomic methods, 6 of the 10 linkage groups had been associated with chromosomes: 2 [*B-lg*], initially incorrectly assigned to 4, 3 [*a1-lg*], 5 [*pr-v2*], 6 [*Y-Pl*], 7 [*gl1-ra*], and 10 [*r-g*]; and

that other methods (*i.e.*, reciprocal translocations) gave a definite check on previous trisomic determinations for linkage groups 1, 4 (*su-Tu*), and 9 (*c-wx*). The early MNLs (1929–1932, reprinted in MNL, Vols. 52–57, 71, and 72) demonstrate McClintock's and other cooperators' contributions to their maize linkage studies.

Continued cooperation throughout the country and the world: The work of maize cooperators stimulated interests in cytogenetics. By 1935 translocations were used to construct many tester lines that contained both phenotypic characters and a translocation. About one-third of the three-point and four-point tests reported in the linkage monograph (EMERSON *et al.* 1935) involved a translocation as a marker. Such translocation-associated three-point tests were extremely valuable, since they allowed confirmation of gene associations with specific chromosomes and gave the order of genes and of cytological locations with translocation breakage points (McCLINTOCK 1931; RHOADES 1931). In addition, CREIGHTON (1934) used pachytene stage chromosomes to continue deletion mapping studies.

Early on, Emerson fostered cooperation among researchers throughout the world. He encouraged both domestic and foreign students to join his research team at Cornell (Figures 3 and 4) and published their findings in the Cooperation's News Letter. Soon, this news circular, which united the maize genetics group, was not limited to offers and demands for strains but also disseminated unpublished results among the researchers. The rule was that any data appearing there could not be cited in publications without the direct consent of the contributor. Maize researchers from around the world—Austria, USSR, Yugoslavia, China, South Africa, Brazil, and Mexico—were honored to share their unpublished results, as we found in MNL reports through 1934.

The first numbered Maize Genetics Cooperation News Letters: The first set of bound News Letters, which we located in the Department of Plant Breeding at Cornell (MNL, Vols. 2–14, 1932–1940), was numbered by hand in pencil, beginning with Rhoades' letter of October 5, 1932, labeled "Vol. 2." This led us to believe that Rhoades' letter was not Maize News Letter 1. These News Letters appear to have been bound and numbered retroactively under the guidance of Emerson, who was the secretary for MNL, Vol. 14, 1940. The "Historical Notes on Maize Cooperation," listed on p. 56, of MNL, Vol. 14, although unsigned, were probably prepared by Emerson, who was secretary for that News Letter. Those notes clearly state that the mimeographed letter of April 12, 1929, is "considered News Letter 1." COE (1976, 1978) used the "Historical Notes" as a guide to compile an archival list of materials of the MNL and related cooperation. While conducting research on the history of maize linkage studies, KASS and BONNEUIL (2004) recently found some of the missing (starred) items on Coe's list. This new information permitted us to recon-

MAIZE GENETICS COÖPERATION

NEWS LETTER

19

February 15, 1945

The data presented here are not to be used in publications without the consent of the authors.

Department of Plant Breeding
Cornell University
Ithaca, N. Y.

FIGURE 5.—Cover of Maize Genetics Cooperation News Letter 19, February 15, 1945. The disclaimer was added to the News Letter cover for the first time in 1945.

struct the historical events leading to the establishment of both the MGC and the MNL and to update and expand the MNL files (COE and KASS 2005). The Plant Breeding Department also has a second set of bound News Letters with similar hand numbering (MNL, Vols. 15–21, 1941–1947); both sets are currently in the custody of Professor Margaret E. Smith on loan to L. Kass). Professor William B. Provine's reprint collection includes a set of unnumbered and unbound News Letters that belonged to Lester Sharp. Sharp's unnumbered collection spans the years 1933–1938 and includes important annotations to linkage in maize. Anderson's and Stadler's unnumbered collections span 1929–1939 and are also annotated. The first covered and hand-numbered News Letter that we found in Cornell's College of Agriculture Mann Library is "Maize Genetics Cooperation News Letter 13, April 15, 1939." Thereafter, the News Letter covers are professionally printed with the title, date, and place of publication—*i.e.*, De-

partment of Plant Breeding, Cornell University. In the reserve copies transferred from Indiana to Missouri in 1974, mimeo copies without covers were on file before 1940, followed by printed-cover copies beginning with Vol. 14. In 1943, Emerson consulted 13 of his most trusted maize cooperators about his concern that some MNL reports had been quoted without permission (Emerson to Cooperators, November 22, 1943, appended to MNL, Vol. 17, 1943, PB). A disclaimer was subsequently added to the News Letter cover in 1945 (Figure 5), and since that time the published covers have not changed with the exception of venue and the contraction to “Newsletter” on the cover beginning in 1990.

CHANGES AND TRANSITIONS IN MAIZE GENETICS COOPERATION

Emerson officially retired in 1941, and thereafter the MNL was edited by his colleagues, students, and occasionally by Emerson himself. He remained active in research until his death on December 8, 1947 (BUSSELL *et al.* 1948). Emerson’s colleagues, former students, and friends contributed to a memorial fund in his name (MNL, Vol. 27, 1953). The funds were applied toward the purchase of a lighted exhibit case placed in the hall of the Plant Breeding Department at Cornell (MNL, Vol. 29, 1955). Part of the exhibit case was used to display continuously some of Emerson’s own work. This case was on the first floor of the Plant Science Building at Cornell until the department moved to Emerson Hall, named for R. A. Emerson, in 1968 (WILLIAMS 1968). One of the authors (L. B. Kass) recalls assiduously exploring this case in the lobby of Emerson Hall when she was a graduate student at Cornell in the 1970s. The case is no longer maintained and its contents and whereabouts are not known at this time.

The Rockefeller Foundation supported the MNL and Stock Center at Cornell through 1953, when funding was withdrawn (MNL, Vol. 27, 1953). Rhoades recognized and confirmed that by the early 1950s scientists at Cornell were ready to forego the Stock Center and News Letter functions when RF withdrew funding, and he arranged to move them to Illinois (see MNL, Vol. 27, pp. 1–2, 1953; Table 3). In 1953, responsibility for the MGC-Stock Center collection moved from Cornell to Illinois, where it was again undertaken by Marcus Rhoades, joined by Earl Patterson (MNL, Vol. 28, pp. 2–10, 1954). Support was provided by the National Science Foundation (NSF) until 1981, following which the U.S. Department of Agriculture supported the program. The Stock Center is now a permanent USDA-Agricultural Research Service program under the direction of Marty Sachs. Its history, catalogs, and ordering procedures are at <http://www.aces.uiuc.edu/maize-coop/>.

After the Rockefeller Foundation withdrew support of the maize cooperation, Cornell funded the MNL

TABLE 3

Transitions of the Maize Genetics Cooperation responsibilities

Years	News Letter	Stocks	Database
1929–1953	Cornell	Cornell	NA
1953–1955	Cornell	Illinois	NA
1956–1957	Illinois	Illinois	NA
1958–1974	Indiana	Illinois	NA
1975–1991	Missouri	Illinois	NA
1991–2002	Missouri	Illinois	Missouri
2003–	Missouri	Illinois	Iowa State and Missouri

from 1953 to 1955, with subsidies from seed companies like DeKalb Agricultural Association; Green Giant; Northrup, King; and Pioneer Hi-Bred Corn (MNL 28: 1, 1954). In 1955, oversight of the MNL moved from Cornell to Illinois under Marcus Rhoades as secretary (MNL, Vol. 30, pp. 1–3, 1956) and it accompanied him to Indiana in 1958 (Table 3). At Illinois funding for the MNL was obtained from seed companies and a grant from NSF. The MNL continued to be edited by Rhoades, aided by Ellen Dempsey (his research associate and former student), as previously, and prepared and distributed at Indiana through 1974. That year the MNL transferred to the University of Missouri, under Edward Coe as secretary, until 2000, when Mary Polacco and Jim Birchler became cosecretaries. The News Letter (now “Newsletter”) continues to be compiled, edited, printed, and distributed at Missouri and is available online at <http://www.maizegdb.org/mnl.php> for previously printed issues or at <http://www.agron.missouri.edu/mnl/> for issues that are in process. Support for its distribution is from an endowment fund established from individual and corporate contributions.

Annual Maize Genetics Conferences were initiated in 1959, following a proposal from John R. Laughnan at the University of Illinois. The conferences are organized and run by a Steering Committee. The 2004 meeting was held in Mexico City. Information about past and future conferences is provided at <http://www.maizegdb.org/cooperators.php>.

The Maize Genome Database (MaizeGDB) was begun in 1991 as an extended medium for communication and for access to data, established by the U.S. Department of Agriculture-Agricultural Research Service at Missouri (USDA-ARS) under the direction of Ed Coe, joined by Mary Polacco. Content of the database, including gene lists, maps, bibliography, and cooperator’s addresses, initially was drawn directly from the files and compilations of the MNL, supplemented by entries of new data. In 2003, the MaizeGDB became a joint endeavor, supported by USDA-ARS, between Missouri (Mary Polacco) and Iowa State University (Volker Brendel, Trent Seigfried, Darwin Campbell, and Carolyn Lawrence). Curation of data content is conducted at the two locations,

and the database is served from Iowa State at <http://www.maizegdb.org/>.

In 2000, a Maize Genetics Executive Committee was elected whose mission is "to identify both the needs and the opportunities for maize genetics, and to communicate this information to the broadest possible life science community. This community includes scientists, funding sources for scientists, and the end users for the accomplishments of maize genetics, from farmers to consumers." Information about the Committee is given at <http://www.maizegdb.org/mgec.php>.

This perspective was developed from a presentation given at the workshop, "The Mapping Cultures of 20th Century Genetics," at The Max Planck Institute for the History of Science, Berlin, Germany, in March 2001. We thank R. MacIntyre for sharing bound and numbered copies of *Drosophila Information Service*, Vols. 1–8, 1934–1937; M. E. Smith for sharing bound and hand-numbered copies of MNL, Vols. 2–14, 1932–1940, and Vols. 15–21, 1941–1947; William Provine for sharing Lester Sharp's unbound and unnumbered copies of MNL, 1933–1938, and for extensive use of his reprint collections; R. P. Murphy for significant insights and encouragement for this project and for sharing his unpublished manuscript on the history of Cornell's Plant Breeding Department; archivists at the Rockefeller Archives Center, Sleepy Hollow, New York, with special thanks going to T. Rosenberg; U.S. National Archives and Records Administration, College Park, Maryland, with special thanks going to J. Schwarz; Division of Rare and Manuscript Collections, Carl A. Kroch Library, Cornell University, with special thanks going to E. Engst; librarians at the Mann Library, especially Tom Clausen; and The L. H. Bailey Hortorium Library, especially P. Fraissinet for bringing many valuable references to our attention. We are grateful to R. P. Murphy, W. B. Provine, and R. H. Whalen for reading early drafts of this article. L.B.K. acknowledges the following for support of archival research: National Science Foundation (grants SBR9511866 and SBR9710488); American Philosophical Society Library, Mellon Resident Research Fellowship; and the Departments of Plant Biology and Plant Breeding and Genetics, Cornell University, Ithaca, New York, for logistical support.

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APPENDIX II

Introduction to Coe, E.H. and L.B. Kass. 2005. *Maize Genetics Cooperation News Letter* files: Expanded chronological list of materials and related cooperation. *Maize Genetics Cooperation Newsletter* 79 (Oct. 31): 72-76; available online April 2005: <http://mnl.maizegdb.org/mnl/79/06CoeKass.htm>

Reproduced in this Appendix is the *MNL* report for the expanded chronological list of archival materials related to the *Maize Genetics Cooperation News Letters* and related cooperation. Based on Emerson's Historical Notes on Maize Genetics Cooperation (*MNL* 14:56), an original list was compiled by Ed Coe, former editor of the *Maize Genetics Cooperation News Letter*, and published in 1976 and 1978. Coe's original list had some items missing from the historical record and, as recorded in this report, Kass and colleagues found some of the missing items. Using many of the archived materials listed in this updated report, Kass et al. (2005, see Appendix I) were able to present an historical perspective of the origin and founding of the *Maize Genetics Cooperation News Letter*. The *Maize Genetics Cooperation News Letter* early volumes reprinted in this two-volume 90th Anniversary book provide documentation for the story told in their historical perspective and in the list provided in the following document.

COLUMBIA, MISSOURI
University of Missouri

ITHACA, NEW YORK
Cornell University

Maize Genetics Cooperation News Letter Files: Expanded chronological list of materials and related cooperation

— Coe, EH; Kass, LB

Based on the “Historical Notes on Maize Genetics Cooperation” (Emerson 1940, MNL 14: 56), Coe compiled an “archival” list of materials of the Maize News Letter and related cooperation (MNL 50:2–4, 1976, MNL 52:146, 1978). While conducting research on the history of maize linkage studies, Kass and Bonneuil (Mapping and seeing: Barbara McClintock and the linking of genetics and cytology in maize genetics, 1928–1935. Pp. 91–118 in H-J Rheinberger and J-P Gaudilliere, eds., Classical Genetic Research and its Legacy: The Mapping Cultures of 20th Century Genetics. London: Routledge, 2004) recently found some of the missing (starred) items on Coe’s lists, and a number of additional documents. We (Kass, Bonneuil, and Coe, in preparation) are currently using these documents to construct a history of the Maize Genetics Cooperation Newsletter in celebration of the 75th anniversary (April 29, 2004) of the MNL.

We present here an expanded, current list of archival materials and cooperation and welcome your contributions towards completing the collections.

Table 1.

PB=Plant Breeding bound volumes, Cornell. MMR=Marcus M Rhoades. LS = Lester Sharp File. RAC = Rockefeller Archives Center. NARA = National Archives and Records Administration.

File No.	PB Vols No.	MNL 14:56 No.	MMR No.	LS Dated	Dated	Pp.	Subject	Reprinted in	
					3/7/23	6	Emerson	Factor Notation.	52:147–149
1a		I.			4/12/29	30	Emerson	Two-page letter, ‘You who attended the “cornfab” in my hotel room at the time of the winter science meetings in New York....,’ linkage group commitments, and a folder of shared linkage information with references. “... considered News letter 1.” [ref. MNL 14:56, and in papers of E. G. Anderson].	53:117–130
1b					11/23/29	2	Beadle	Assembling Linkage Data [Brink Papers, U of WI Archives].	72:129–130
1c					12/19/29	1	Beadle	Summarization of Linkage — Request for Data.	54:136
1d					2/5/30	1	Beadle	Summarization of Linkage — Request for Data.	54:136
2a.1		II.			4/17/30	17	Emerson	Revised maps [“second folder of mimeo” Exhibit D found at RAC, and in papers of E. G. Anderson].	54:136–139
2a.2		II.			7/26/30	23	Emerson	Linkage data [“second folder of mimeo” Exhibit D found at RAC, and in papers of E. G. Anderson].	54:140–145
					11/18/31	1	Emerson	Call for Linkage Data [PB Records, Cornell Archives]; “Records should be sent to Dr. G. W. Beadle” at Caltech.	71:119
2b		II.			8/26/32		Emerson?	Cooperation planned at VI Cong (ref. MNL 14:56) [“Cooperation of maize geneticists planned at ... congress”; Genetics Congress held at Ithaca in August 1932 — Historical Notes in MNL 14:56]; this apparently does not refer to a written item, but a report/summary of meeting held on 26 August 1932 is included as part of Rhoades’ letter of 10/5/1932 [Exhibit C RAC].	
2c	Vol. 2, 1932	II.	1		10/5/32	3	Rhoades	Congress Report [“action taken at Genetics Congress. Chromosomes assigned to different individuals.” — MNL 14:56], Stocks appeal [RAC, Exhibit C in part].	56:173–174
2d	[3]*	II.			12/12/32	1	Rhoades	Call for stocks contributions and wants, and for news items “so that we may list your contributions and wants in the corn-letter which will come out in the near future”, request for data to include in the linkage summary; Exhibit IV cited in 1933 NRC grant, see below.	57:192
3a	Vol. 3	III.	2	1/23/33	1/23/33	16	Rhoades, RAC, Exhibit C in part	Wants, Symbols, Stocks, Genelist [“Third Corn News Letter ...Long list of known genes of maize,” — MNL 14:56] “(MNL 3)” [“Exhibit V” cited in 1933 NRC grant — see below — and included in Exhibit C, RF grant 1934].	57:192-200
2e		II.			1/?/1933			Grant Support [ref MNL 14:56]. Emerson submitted the NRC grant in January of 1933, see MNL 14:56, correspondence by Emerson about possible grant of money for Maize Cooperation, Jan. 1933. Exhibit V = Rhoades 1/23/1933, cited in NRC grant, 1933 and included with Exhibit C, RF grant, 1934].	
					3/17/33		RAC, Exhibit B	NRC grant — Report of the Committee on Agronomy of the Division of Biology and Agriculture NRC to support “A Clearing House for Corn Genetics Materials and Information,” dated March 17, 1933 (found at RAC); Committee recommended but NRC did not approve grant to Emerson; “The project has been set up and is active (Exhibits II, III, IV & V)”; Note exhibits I–IV are not in the file but Exhibit IV is clearly Rhoades’ call of 12/12/32; and Exhibit V is Rhoades’ 1/23/1933, which we identified from Anderson’s copy (reprinted in MNL 57:192-200)].	
3b	[4]	III.	3		11/13/33	2	Rhoades	“This letter is a call for information to be used in succeeding corn letters. We thought it would be appropriate if the first letter in the fall of each year presented new and pertinent information of value to all maize investigators, such as new linkages, ...” Deadline January 15.	
4	Vol. 4	IV.	4	12/18/33	12/18/33	7	Rhoades	News [“Many news items contributed by cooperators,” — MNL 14:56; “Letter of 12 pages” (sic)].	
					12/26/33			NRC application denied (Exhibit A, RAC).	
5	Vol. 5	V.	5	1/25/34	1/25/34	12	Rhoades	Nomenclature, Stocklist [“Big Inventory of corn,” — MNL 14:56] [Exhibit J, RAC].	
					2/6/34		CU, RAC	Emerson applies to Rockefeller Foundation for grant to support Maize Genetics Cooperation.	
6	Vol. 6	VI.	6	2/21/34	2/21/34	4	Rhoades	Nomenclature [“Discussion of nomenclature,” — MNL 14:56].	
					3/16/34		RAC	\$5,000 Rockefeller Grant-in-aid for pure research and a clearing house for corn genetics (RAC).	
					3/22/34		Emerson	Emerson to about 15 “cooperators who have contributed unpublished data for a summary of linkage in maize: ... I desire to know whether you are now willing to allow publication from Cornell of your as yet unpublished data which are included in the [mimeographed linkage] summary.” [NARA].	
		VI.			4/1/34			Rockefeller Grant [“April 1, 1934, RF Grant available,” ref MNL 14:56; grant found at RF, see above].	
7	Vol. 7	VII.	7	9/13/34	9/13/34	11	Rhoades	Call, News, Genelist, Mailing list of 39 maize geneticists plus 21 others who asked to receive the news letter; announcement of RF grant for 5 years, no date identified when grant began.	
					9/13/34		Russia	Reference made to 1930 “Linkage in Maize” (MNL 7:3, 1934; see 7/26/30).	
8	Vol. 8	VIII.	8	11/24/34	11/24/34	18	Rhoades	News.	
9c	[9]				1/21/35	1	Rhoades	“... call for lists of new genetic stocks, news items, etc., for another corn letter which will be issued around the first of March.” Deadline February 15.	
9	Vol. 9	IX.	9	3/6/35	3/6/35	22	Rhoades	Stocks, News, Map [20 numbered pages plus unnumbered 3 pages of methods by Randolph; plus Rhoades note (“The enclosed maps of linkage groups were made from the data which Emerson has assembled for the forthcoming paper on linkages in maize by Emerson, Beadle and Fraser”) and a map (“CHROMOSOME MAPS OF MAIZE 1935”)]. [Sharp’s copy has 20 numbered pages plus Rhoades’ note following the last numbered page (p. 20) but is missing the linkage map; Anderson’s copy is like PB vol. 9; PB vol. 9 includes 25 pages (20+2+3), of which the last 3 pages are Emerson’s letter of November 30, 1935; see below].	
10b					9/17/35	1	Emerson	Disease resistance test cooperation requested [half-sheet; not in PB volume].	
10c	[9]			11/30/35	11/30/35	3	Emerson	Call for news items; summary of linkage in maize off the press; cooperative disease resistance tests; collective short publications on linkage proposed [Emerson signs as secretary “pro tem”; Exhibit “B” at top of page in green ink (and crossed out) in Emerson’s handwriting (no department number); used to document Emerson’s RF grant report — in pencil is “Put after vol 9 before Vol 10”; Sharp’s copy has	

							dept. no. 757 at top left but no Exhibit letter at the top of Sharp's copy].
10	Vol. 10	X.	3/4/36	3/4/36	22	Emerson	News, Data, Stocks, Inbred tests.
11c	[11]			11/21/36	1	Langham	Call, deadline January 15.
11d	[11]			1/5/37	1	Langham	Call, deadline January 15.
11	Vol. 11	XI.	3/23/37	3/23/37	26	Langham	News, Stocks, Inbred tests.
12c	[12]			11/17/37	2	Langham	Call, deadline January 15; encouragement of collective short proposals on linkage.
12d	[12]			1/22/38	1	Langham	Call, deadline advanced to February 15, 1939.
							News, Stocks, Symbol Index for 1/23/33-3/6/38; Maps by Langham, hand-drawn (A "showing the loci of those genes whose position can be determined with reasonable certainty"; B "showing the approximate loci of many genes. (Working map. More 3-point tests needed ...) [at end of PB volume and in Anderson copy; Sharp's copy, p. 38 is last page — chromosome linkage maps are missing; Sharp's last un-numbered copy is dated March 6, 1938].
12	Vol. 12	XII.	3/6/38	3/6/38	40	Langham	Call.
13c	[13]			1/21/39	1	Langham	News, Stocks, Bibliography, Mailing list of 77 persons, 20 outside of the US. Mann Library numbered copies begin with no. 13 [April 15, 1939]; the first bound Plant Breeding volume ends with volume 14, March 5, 1940; The second bound Plant Breeding volume ends with volume 21, March 1, 1947 ["MNL, Vols. 2-14, 1932-1940," & "MNL Vols. 15-21, 1941-1947" (PB)] There are no covers included in the PB bound volumes, only blue pieces of paper separating volumes. — LBK checked the bound volumes at Mann Library; manila folder cover hand written title and number 13 on cover. Anderson copies through this date are unnumbered.
13	Vol. 13	XIII.		4/15/39	22	Langham	Call for 1940 MNL; deadline January 15.
14c	[14]			10/31/39	1	Lebedeff	Call reminder, half sheet [Not in PB bound volumes].
14d	Vol. 14	XIV.		1/8/40	1	Emerson	News, Bibl, Stocks (by Lebedeff), Historical Notes on Maize Genetics Cooperation I-XIV on page 56 likely by Emerson [last 3 pages in PB volume 14 are letter of 2/5/41 and "An Appreciation" of Emerson, see below] [Mann Library Copy, L.J. Stadler copy, and E.G. Anderson copy have only the 56 pgs]. Professionally printed, numbered covers begin with vol. 14.
14	[14]			3/5/40	56+(3)	Emerson	Call for 1941 MNL; deadline March 1.
15c	[15]			1/21/41	1	Fraser	Letter, Emerson's retirement and reunion of maize genetics workers: "As you may know Dr. Emerson reaches retirement age this coming June ... this coming summer is an appropriate time to hold a reunion of his former students and coworkers in corn genetics. Preliminary arrangements are now being made for such a reunion to be held at Ithaca in late August or early September, either just before or just after the summer meeting of the Genetics Society at Cold Spring Harbor." List of 30 names to whom this invitation is sent appended below and those (11) who have already indicated they would attend are starred.
				2/5/41	1	Randolph, Fraser	News, Editorial Policy of GENETICS (Rhoades), Stocks, chromosome assignments, Bibliography [Mann Library copy, Anderson copy, and Stadler copy have "An appreciation" of 2 pgs. preceding pg. 1 within the manila cover and affixed with brass round-headed paper fasteners; see above, vol. 14].
15	Vol. 15			4/1/41	(2)+56	Fraser	Call; deadline January 15.
16c	[16]			12/10/41	1	Emerson	[Plus Table of Contents] note in memory of Fraser by Emerson; Reports, Stocks (by Einset, Welch), Bibliography (by Emerson).
16	Vol. 16			2/10/42	i+59	Emerson	Call; deadline January 31.
17c	[17]			12/10/42	1	Emerson	Reports, Stocks, Bibliography [plus 1 pg. 11/22/43 Emerson to 11 cooperators-see below][Only the year is listed on PB copy, Vol. number not hand written in this or subsequent bound PB volumes].
17	Vol 17, 1943			2/15/43	51+(1)	Emerson	LBK found in PB copy at end of vol. 17, 1943. "This is being sent to" [13 cooperators]. Emerson upset that News Letter was quoted without permission, "Should we send the newsletter only to workers in maize genetics".
	[17]			11/22/43	1	Emerson	Assumed Call for 1944, no copy found.
				[1943]			[Plus Table of Contents] Reports, Stocks, Bibliography (by A.M. Brown).
18	Vol. 18			1/31/44	i+32	Emerson	Assumed Call for 1945, no copy found.
				[1944]			Reports, Stocks (Cushing, Morris), Bibliography [disclaimer added to cover: "The data presented here are not to be used in publications without the consent of the authors"].
19	Vol. 19			2/15/45	i+50	Cushing	Assumed Call for 1946, no copy found.
				[1945]			Reports, Stocks (Cushing, Morris), Bibliography (by Smith) [pg 2 has an announcement by Emerson, "Arrangements have been made to continue the Maize Genetics Cooperation at Cornell University for a period of not less than three years. Professor R. L. Cushing, who has been responsible for the work done during the past few years, will help initiate Prof. H. H. Smith who will have charge of the work in the immediate future.... R. A. Emerson."]. [disclaimer is emphasized by addition of a box border].
20	Vol. 20			4/15/46	i+35	Cushing	Call for 1947 MNL; deadline February 15.
21c	[21]			12/26/46	1	Smith	[Plus Table of Contents]. Reports, Bibliography [Last PB bound volume, volume 21, March 1, 1947][[disclaimer is further emphasized by a double box border].
21	Vol. 21			3/1/47	i+59	Smith	Death of Emerson, Dec. 8, 1947; end of PB bound Maize Newsletters is 1947.
				12/8/47			Call for 1948 MNL; deadline February 15.
22c				12/17/47	1	Smith	Note in memory of Emerson by L. F. Randolph, B.S Monroe, & F. P. Bussell, Reports, Stocks (by Wright), Bibliography (by Wright).
22				3/8/48	i+72	Smith	Call for MNL 23, 1949; deadline February 15.
23c				12/28/48	1	Smith	Note in memory of Lindstrom by J. W. Gowen; Reports; Stocks (by Wright); Bibliography (by Wright).
23				3/10/49	i+78	Smith	Assumed Call for 1950, no copy found.
				[1949]			Reports, Stocks (by Craigiles), Bibliography.
24				3/17/50	i+81	Smith	Assumed Call for 1951, no copy found.
				[1950]			Reports, Historical, Author index vol. 9-24, Stocks (by Craigiles), Bibliography (by Craigiles).
25				3/17/51	i+68	Smith	Call for MNL 26, 1952; deadline February 15.
26c				1/2/52	1	Smith	Report on meeting to discuss Support for the Coop at AIBS Meetings in Minnesota September 12, 1951 (Smith); Reports, Stocks (by Craigiles), Bibliography (by Woodward, Craigiles).
26				3/17/52	i+76	Smith	Stock Center, Project Outline.
27b				9/26/52	4	Rhoades	Call for MNL 27, 1953; deadline February 15.
27c				12/30/52	1	Smith	Report on meeting to discuss support for the Coop at AIBS Meetings at Cornell September 9, 1952 (Laughnan); Reports, Bibliography (by Sherwood).
27				3/17/53	i+90	Everett	Call for MNL 28; deadline February 15.
28c				1/5/54	1	Smith	Funds received from hybrid corn companies to support MNL; Reports, Stocks (Patterson), Bibliography (Wright).
28				3/17/54	ii+94	Smith	

29c	12/15/54	2	Smith	Call for MNL 29, 1955 with example; deadline February 15.
29	3/17/55	ii+100	Smith	Reports, Stocks (Patterson), Bibliography (Wright).
30c	12/7/55	1	Rhoades	Call for 1956 MNL (from Illinois); deadline February 15; Transfer of MNL Responsibility.
30	3/15/56	ii+164	Rhoades	Minutes of 1955 meeting of maize geneticists at AIBS meetings at Michigan State University regarding transfer of Stocks and the Maize Genetics Cooperation Newsletter, chromosome responsibilities (Patterson); Reports, Stocks (Patterson), Bibliography (Bibl.) [News Letter published in Department of Botany, University of Illinois].
31c	12/7/56	1	Rhoades	Call for 1957 MNL; deadline February 15.
31	3/15/57	ii+173	Rhoades	Nomenclature, Reports, Stocks, Bibl.
32c	12/12/57	1	Rhoades	Call for 1958 MNL (from Illinois); deadline February 15.
32	3/15/58	ii+156	Rhoades	Reports, Stocks, Bibl. [published in Department of Botany, Indiana University][Seed companies fund publication of MNL; Obituary of Frederick David Richey (1884–1955) by H. K. Hayes].
33c	12/8/58	1	Rhoades	Call for 1959 MNL, deadline February 15 (from Indiana).
33	4/1/59	ii+168	Rhoades	Reports, Stocks, Bibl., Mailing list.
34c	12/8/59	1	Rhoades	Call for 1960 MNL, deadline February 15.
34	5/1/60	ii+154	Rhoades	Reports, Stocks, Bibl. [Rhoades incorporates a Foreword to the News Letter and acknowledges Ellen Dempsey "who has been largely responsible for assembling the News Letter."][Indiana University and NSF grant (in part) fund publication of MNL].
35c	12/9/60	1	Rhoades	Call for 1961 MNL, deadline February 15.
35	4/15/61	ii+183	Rhoades	Reports, Stocks, Bibl. [NSF grant funds publication of MNL].
36c	12/8/61	1	Rhoades	Call for 1962 MNL, deadline February 15.
36	4/15/62	ii+122	Rhoades	Reports, Stocks, Bibl.
36i	7/1/62	45	Coe	Symbol Index, MNL 12–35 (from Missouri).
37c	12/1/62	1	Rhoades	Call for 1963 MNL, deadline February 15.
37	4/15/63	ii+196	Rhoades	Reports, Chromosome 1 Data, Stocks, Bibl.
38c	12/6/63	1	Rhoades	Call for 1964 MNL, deadline February 15.
38	4/15/64	ii+150	Rhoades	Reports, Stocks, Bibl.
39c	12/14/64	1	Rhoades	Call for 1965 MNL, deadline February 15.
39	4/15/65	ii+210	Rhoades	Reports, Stocks, Bibl.
40c	12/14/65	1	Rhoades	Call for 1966 MNL, deadline February 15.
40	4/15/66	ii+205	Rhoades	Reports, Map, Stocks, Bibl.
41c	12/21/66	1	Rhoades	Call for 1967 MNL, deadline February 15.
41	4/15/67	ii+233	Rhoades	Reports, Stocks (Lambert), Bibl.
42c	12/15/67	1	Rhoades	Call for 1968 MNL, deadline February 15.
42	4/15/68	iii+208	Rhoades	Reports, Stocks, Bibl.
43c	12/15/67	1	Rhoades	Call for 1969 MNL, deadline February 15.
43	4/15/69	ii+242	Rhoades	Reports, Stocks, Bibl.
44c	12/18/69	1	Rhoades	Call for 1970 MNL, deadline February 15.
44i	4/15/70	51	Coe	Author and Name Index, MNL 3–43 (from Missouri).
44	4/15/70	ii+232	Rhoades	Reports, Stocks, Bibl.
45c	12/18/70	1	Rhoades	Call for 1971 MNL, deadline February 15.
45	4/15/71	ii+287	Rhoades	Reports, Stocks, Bibl.
46c	12/6/71	1	Rhoades	Call for 1972 MNL, deadline February 15.
46	4/15/72	ii+245	Rhoades	Reports, Stocks, Bibl.
47c	12/12/72	1	Rhoades	Call for 1973 MNL, deadline February 15.
47	4/15/73	ii+277	Rhoades	Reports, Nomenclature, Stocks, Mailing list, Bibl.
48c	12/12/73	1	Rhoades	Call for 1974 MNL, deadline February 15.
48	5/15/74	ii+244	Rhoades	Reports, Stocks, Bibl.
49c	1/13/75	1	Coe	Call for MNL 49, deadline February 15 (from Missouri); transfer of responsibility.
49	4/15/75	ii+183	Coe	Reports, Stocks, Bibl. [Published at University of Missouri].
50c	11/1/75	1	Coe	Call for MNL 50, 1976, deadline January 1.
50	3/1/76	ii+180	Coe	Reports, Stocks, Bibl., Mailing list, Author Index [Chronological list of News Letter Files].
51c	11/1/76		Coe	Call for MNL 51, 1977, deadline January 1.
51	3/1/77	ii+126	Coe	Reports, Stocks, Bibl., Author Index (AI), Maps.
52a	4/4/77	2	Coe	Request for Cytogenetic Working Map data by October 1.
52b	9/19/77	2	Coe	Reminder for Cytogenetic Working Map data.
52c	11/5/77	1	Coe	Call for MNL 52, 1978, deadline January 1.
52	3/1/78	ii+178	Coe	Reports, Cytogenetic Maps, Stocks, Bibl., Symbol index (SI), AI, News Letter Files list additions, 55 Years reprinted (3/7/23).
	4/25/78	1	Coe	Request for Cytogenetic Working Map data by October 1.
	11/1/78	1	Coe	Call for 1979 MNL, deadline January 1.
53	3/1/79	ii+166	Coe	Reports, Stocks, Bibl., Mailing list, SI for MNL 36–53, AI, 50 Years reprinted (4/12/29).
	4/12/79	1	Coe	Request for mapping work and new data.
	11/9/79	1	Coe	Call for 1980 MNL, deadline January 1.
54	3/31/80	ii+163	Coe	Reports, Zealand, Stocks, Bibl., Mailing list, SI, AI, 50 Years reprinted (12/19/29, 2/5/30, 4/17/30, 7/26/30).
	11/5/80	4	Coe	Stock Center support from USDA; Questionnaire on MNL features and on Stock Center functions.
	11/15/80	1	Coe	Call for 1981 MNL, deadline January 1.
55	3/15/81	iii+161	Coe	Reports, Zealand, Stocks, Bibl., SI, AI.

56	11/20/81	1	Coe	Call for 1982 MNL, deadline January 1.
	3/2/82	1	Coe	Plan for meeting on mapping.
	3/15/82	iv+208	Coe	Reports, Zealand, Stocks, Mailing list, Bibl., SI, AI, 50 Years reprinted (10/5/32).
	4/22/82	30	Coe	Planning with Mapping Coordinators; data compilations.
57	12/1/82	1	Coe	Call for 1983 MNL, deadline January 1.
	3/3/83	4	Coe	Planning with Mapping Group; data compilations for 1983.
	3/31/83	iv+236	Coe	Reports, Zealand, Genelist & Maps, Stocks, Bibl., Mailing list, SI, AI, 50 Years reprinted (12/12/32, 1/23/33).
	8/5/83	3	Coe	Coordination of mapping, chromosome responsibilities.
58	10/31/83	1	Coe	Request to Mapping Coordinators for summarized reports by January 1.
	11/23/83	1	Coe	Call for 1984 MNL, deadline January 1.
	4/30/84	vi+258	Coe	Reports, Mapping, Zealand, Stocks, Bibl., Mailing list, SI, AI, Maps.
	11/8/84	1	Coe	Call for 1985 MNL, deadline January 1.
59	1/10/85	1	Coe	Request to Mapping Coordinators for summarized reports.
	3/31/85	iv+187	Coe	Reports, Mapping, Zealand, Stocks, Mailing list, Bibl., SI, AI, Cytogenetic Data, Maps.
	11/15/85	2	Coe	Call for MNL 1986, deadline January 1; request to send stocks to Stock Center; information on integrated mapping.
	11/29/85	15	Coe	Minutes of National Plant Genetic Resources Board re mapping integration for maize.
60	1/21/86	1	Coe	Request to Mapping Coordinators for summarized reports.
	3/12/86	1	Coe	Planning with Mapping Group for meeting on mapping.
	3/31/86	viii+212	Coe	Reports, Zealand, Stocks, Mapping, Mailing list, Bibl., SI, AI.
	11/15/86	2	Coe	Call for 1987 MNL, deadline January 1.
61	1/13/87	1	Coe	Request to Mapping Coordinators for summarized reports.
	3/31/87	iv+177	Coe	Reports, Zealand, Stocks, Mapping, Mailing list, Bibl., SI, AI.
	11/15/87	2	Coe	Call for 1988 MNL, deadline January 1.
	1/20/88	1	Coe	Change to require Subscriptions and Endowment.
62	3/31/88	iv+179	Coe	Reports, Zealand, Stocks, Mapping, Genelist, Maps, Mailing list, Bibl., SI, AI.
	11/21/88	1	Coe	Call for 1989 MNL, deadline January 1; Maize Conference news.
63	3/31/89	xi+195	Coe	Reports, Zealand, Stocks, Mapping, Mailing list, Bibl., SI, AI, Donors.
	11/15/89	1	Coe	Call for 1990 MNL, deadline January 1; Maize Conference news.
64	3/31/90	ix+208	Coe	Reports, Zealand, Stocks, Genelist, Maps, Mailing list, Bibl., SI, AI, Donors.
	11/15/90	1	Coe	Call for 1991 MNL, deadline January 1; Maize Conference news.
65	3/1/91	viii+212	Coe	Reports, Zealand, Stocks, Genelist, Maps, Mailing list, Bibl., SI, AI, Donors.
	3/15/92	x+220	Coe	Reports, Zealand, Stocks, Genelist, Maps, MaizeDB, Mailing list, Bibl., SI, AI, Donors; Rhoades memory by Dempsey.
67	11/10/92	1	Coe	Call for 1993 MNL, deadline January 1; Maize Conference news; Marty Sachs to head Maize Genetics Cooperation — Stock Center.
	3/15/93	vii+231	Coe	Reports, Zealand, Stocks, Genelist, Maps, MaizeDB, Mailing list, Bibl., SI, AI, Donors; MaizeDB report and access through Gopher; issue dedicated to McClintock, references to essays and memories.
	11/1/93	1	Coe	Call for 1994 MNL; access available through Gopher, AceDB, WWW, and MaizeDB; Maize Conference news; Patterson retires from responsibilities with the Stock Center, Stinard Curator.
	3/15/94	vii+253	Coe	Reports, K-12, Mailing list, Stocks, Zealand, Nomenclature, Genelist, Maps, MaizeDB, Bibl., SI, AI, Donors.
68	12/14/94	2	Coe	Call for 1995 MNL by email; access available through Gopher, AceDB, WWW, and MaizeDB; Maize Conference news.
	12/14/94	1	Coe	Call for 1995 MNL; access available through Gopher, AceDB, WWW, and MaizeDB; Maize Conference news.
	8/15/95	viii+321	Coe	Reports, K-12, Mailing list, Stocks, Nomenclature, MaizeDB, Probe Bank, Genelist, Maps, Zealand, Bibl., SI, AI, Donors.
	11/13/95	1	Coe	Call for 1996 MNL; Maize Conference news.
70	3/15/96	v+185	Coe	Reports, Mailing list, Stocks, MaizeDB, Probe Bank, Genelist, Maps, Zealand, Bibl., SI, AI, Donors.
	10/22/96	2	Coe	Call for 1997 MNL by email; initiation of Virtual MNL, Verbatim incorporation, and Linkletter.
	11/13/96	1	Coe	Call for MNL 71 by postcard.
	4/15/97	iv+126	Coe	Reports, K-12, Mailing list, Stocks, MaizeDB, Probe Bank, SI, AI, Donors; 66 Years reprinted (11/18/31).
71	8/20/97	1	Coe	Call for MNL 72, 1998 on web in MaizeDB; Virtual MNL, Verbatim incorporation, and Linkletter.
	12/3/97	1	Coe	Call for MNL 72, 1998 by postcard.
	12/3/97	1	Coe	Call for MNL 72, 1998 by email; Maize Conference news.
	4/15/98	iv+134	Coe	Reports, Mailing list, Stocks, MaizeDB, Probe Bank, Maps, SI, AI, Donors, 69 Years reprinted (11/23/29).
72	11/30/98	1	Coe	Call for MNL 73, 1999 by email; Maize Conference news.
	4/15/99	iv+155	Coe	Reports, Mailing list, Stocks, MaizeDB, SI, AI, Donors.
	11/29/99	2	Coe	Call for 2000 MNL by email; Maize Conference news.
	4/15/00	x+116	Coe	Reports, Mailing list, Stocks, MaizeDB, SI, AI, Donors; Li Jing Xing (C.H. Li) memory by Chase; Patterson memory from Illinois.
73	11/17/00	1	Birchler, Polacco	Call for MNI 75, 2001 by email.
	11/17/00	1	Polacco, Birchler	Call for MNL 75, 2001 on web in MaizeDB.
	11/21/00	1	Coe	MNL self-supporting, change in subscription policy; MNL 59 and above in MaizeDB.
	8/15/01	vii+131	Polacco, Birchler	Reports, Mailing list, Stocks, MaizeDB, SI, AI, web sites, Maize Genetics Executive Committee, sequencing report; transfer of responsibility for MNL to Polacco and Birchler.
74	[2001]		Polacco, Birchler	Call assumed.
	5/15/02	vi+148	Polacco, Birchler	Reports, Mailing list, Stocks, MaizeDB, SI, AI; Nelson memory by Hannah, Burr, Dooner.

77	11/30/02	1	Polacco, Birchler	Call for 2003 MNL by email.
	7/29/03	iii+183	Polacco, Birchler	Reports, Mailing list, Stocks, MaizeDB, SI, AI; recent Donors.
	12/8/03	1	Birchler, Polacco	Call for 2004 MNL by email.
78	7/26/04	iii+163	Polacco, Birchler	Reports, Address List, Stock Center, Community IBM (cIBM) Maps, Recent Maize Publications, SI, AI

* numbers in brackets represent the volume with which that communication was bound in the PB set — i.e., Rhoades call of 12/12/32 was bound with Volume 3, 1/23/33.

LBK acknowledges the National Science Foundation (grants SBR9511866 and SBR9710488), for support of archival research; the Departments of Plant Biology and Plant Breeding at Cornell University for logistical support; with grateful thanks to Chris Bonneuil, Royse P. Murphy, William B. Provine, and Margaret Smith, for sharing notes and documents in the spirit of maize cooperation; to archivists Thomas Rosenbaum, RAC and Joseph Schwarz, NARA, for permission to use the collections and for supplying information and copies of letters, and to Mary L. Polacco for encouragement and aid in systematizing the information.

Please Note: As is the policy with the printed version, notes submitted to the Maize Genetics Cooperation Newsletter may be cited only with consent of the authors.

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APPENDIX III

Contributor's Biographical Sketches

Editors:

Dr. Lee B. Kass received her Ph.D. in botany and genetics from Cornell University (1975), and earned a B.S. in biology at The City College of New York (CUNY, 1969). She did postdoctoral research at The University of Cambridge (UK) and Vanderbilt University. She has served on the faculties of The University of Cambridge (UK), University of Tennessee (Nashville), Elmira College (New York), The College of the Bahamas (Nassau), Cornell University, and West Virginia University (Morgantown). Kass has authored, edited or co-edited ten books, and authored or co-authored more than 90 book chapters, proceedings papers, and articles in scientific journals. She is a member of the Botanical Society of America, The Bahamas National Trust, and a former member of many botanical organizations. Kass was chair of the Historical Section of the Botanical Society of America for many years. She established the Elmira College Herbarium in 1985, and currently serves on the Science Advisory Committee of the Bahamas National Trust. Among her awards is the Josef Stein Award, for excellence in teaching and scholarly achievement (1985) and a Fulbright Scholar Award (1996), during which time she and her spouse, Dr. Robert E. Hunt, established the National Herbarium of the Bahamas. She is Visiting Professor at Cornell University, and West Virginia University (Morgantown). Her research focuses on history of botany, and biodiversity and reproductive biology of Bahamian plants.

Dr. Edward H. Coe Jr. earned a Ph.D. (1954) in botany at the University of Illinois (with John Laughnan) and received his M.S. degree (1951) in plant genetics (with Charlie Burnham), and a B.S. degree (1949) in agronomy and plant genetics from the University of Minnesota. Following a postdoc with Ernest G. Anderson at Caltech (1954-1955), Coe joined the Plant Genetics Unit of the U.S. Department of Agriculture-Agricultural Research Service at the University of Missouri, where he is currently Professor Emeritus of Plant Sciences. His research has contributed to an understanding of anthocyanin biosynthesis, gametophyte functions, non-Mendelian inheritance, and extrachromosomal inheritance. He is author of or co-author of over 100 refereed journal articles, and author or co-editor of two books; most well-known is the co-edited *Mutants of Maize*. Coe is highly appreciated for his 26 years of continuous service as editor of the *Maize Genetics Cooperation Newsletter* (1974-2000). He played a central role in establishing the Maize Genome Database and in the early planning meetings leading to sequencing of the first plant genome, the maize genome. He is a member of various professional organizations, including the Genetics Society of America, the American Genetic Association, and the Crop Science Society of America. In recognition of his "lifetime contributions to the field of genetics," Coe was awarded the prestigious Thomas Hunt Morgan Award by the Genetics Society of America in 1992. The award was presented to him in recognition of the importance of his basic research, his mentorship of students and postdocs, and his extensive and outstanding service to the maize genetics community. Dr. Coe was described as "the glue that holds the maize community together." At the 2018, 60th Annual Maize Genetics Conference, held at Palais du Grand Large, Saint-Malo, France, Coe was honored with the newly established R.A. Emerson Award, which recognizes individuals for their extraordinary lifetime achievements in maize genetics. Recipients of this award are leaders in the maize community, who have made seminal contributions to our understanding of maize genetics. Coe's Emerson Award was presented at the March 2019 Maize Genetics Conference in Saint Louis, along with a short overview of his life and work. In April 2019, the Academy of Science – St. Louis honored Coe with The Peter H. Raven Lifetime Achievement Award, which recognizes a distinguished career of service in science, engineering, or technology.

Michael N. Cook is a Librarian whose MLIS degree (1997) and MA degree in philosophy (1994) are from the University of South Carolina, with a B.A. degree in English (1990) from Western Carolina University. He is the Head of Collections at Cornell University's Albert R. Mann Library. His areas of expertise include collection development, digital preservation, copyright, open access, digital repositories, special collections and rare books, and scholarly communication. Michael was the 2007 recipient of the State University of New York (SUNY) Chancellor's Award for Excellence in Librarianship and also received the 2017 Melanie Gardner Agriculture Network Information Collaborative (AgNIC) Distinguished Service Award.

Dr. Margaret E. Smith received her Ph.D. (1982) in Plant Breeding and Genetics from Cornell University. She subsequently worked as a plant breeder at the Tropical Agricultural Center for Research and Teaching (CATIE) in Costa Rica, and then ran a successful corn breeding program at the International Maize and Wheat Improvement Center (CIMMYT). Smith returned to Cornell in 1987 as an Assistant Professor of Plant Breeding & Genetics to head the corn breeding research project. She is now Professor and also the Associate Director of the Cornell University Agricultural Experiment Station. Her research goal is to enhance an understanding of corn adaptation to marginal environments and develop genetic materials that will improve corn productivity and sustainability in such environments. She assumed responsibility in 2004 as Extension Leader for Plant Breeding and Genetics, focusing on public education about plant breeding, variety testing, and seed issues. Smith is the Project Leader for the New York Seed Improvement Program of Plant Breeding and Genetics. She oversees the Corn Variety Testing program, which aims to evaluate hybrids over a range of environments in New York. She also teaches about genetically engineered crop plants (basic public issues education) and agriculture in the developing world. She has trained more than 20 Ph.D. students, and six Masters students. She was the recipient of the Outstanding Faculty Award (2015) from the College of Agriculture and Life Sciences Alumni Association and the College of Agriculture and Life Sciences (CALS) 2012 Outstanding Service to CALS award.

Judy L. Singer received her BA (1977) in Sociology/Anthropology, from Ithaca College. She began working at Cornell Plant Breeding for Professor and Department Extension Leader William D. Pardee in 1976, as a Secretary, then as an Extension Support Aide, and finally as an Extension Support Specialist. For 25 years she traveled the state of New York for the New York Hybrid Corn Performance Trials testing program participating in all aspects of field testing operations, collecting, compiling, analyzing data, and producing final reports. She later worked with Margaret Smith, and other Plant Breeding faculty members affiliated with the applied Plant Breeding programs. Judy helped Dr. Pardee to organize the 75th Synapsis Club Reunion (1982). She had organized, and saved, most of the files from that event, which later proved invaluable to the publication of the Department's Centennial History. She co-served as a production coordinator for the print version of the 2007 Centennial History book, and proof read the hard copy and later the e-book. She was also a member of the committee to organize former Plant Breeding Department Chair (1956-1979) R.P. Murphy's 90th birthday celebration (May 2, 2004). For that event she organized family photographs, helped to coordinate events, and compiled the *Memory Book* of the event. She proofread for the McClintock Perspectives *Companion Volume*, edited by Kass. Judy retired from her permanent Cornell appointment in 2009 and was asked to return in a part time Temporary Service Professional position. On 29 November 2017, Judy received the first Chair's *Award for Excellence*, for her 33 years of full time service to Plant Breeding & Genetics. She continues to work closely with the Plant Breeding & Genetics designated historian, Dr. Lee B. Kass, to save files of historical significance to the history of one of Cornell's most notable Departments.

Foreword Contributor:

Dr. Edward S. Buckler received his Ph.D. (1997) in biological sciences from the University of Missouri-Columbia. He served as research geneticist, U.S. Department of Agriculture - Agricultural Research Service (USDA-ARS), and Adjunct Assistant Professor of Genetics at North Carolina State University, Raleigh, from 1998 to 2003, before starting at the USDA/ARS Robert W. Holley Center for Agriculture and Health, at Cornell's Institute for Genomic Diversity in 2003. Buckler is a Research Geneticist with the Senior Scientific Research Service, USDA-ARS, and an Adjunct Professor of Plant Breeding & Genetics at Cornell. He is recognized as a leader in the integration of quantitative and statistical genetics with genomic approaches, whose work has deepened our understanding of the control of crop complex traits, and applying those superior genetic variations to crop improvement. Subsidized by the United States Department of Agriculture and National Science Foundation, he has led the largest maize research team in the US, achieving more than 200 periodical publications, including *Science*, *Nature*, *Nature Genetics*, *PNAS*, *Plant Cell*, *Nature Review Genetics* and *Nature Communications*. He has had the pleasure of mentoring over 50 postdocs and graduate students. In 2014, Buckler was elected to the U.S. National Academy of Sciences (NAS), Section of Plant, Soil, and Microbial Sciences. He was the recipient of the 2017, NAS Prize in Food and Agricultural Sciences, the first time this prize was awarded. This prize recognizes research by a mid-career scien-

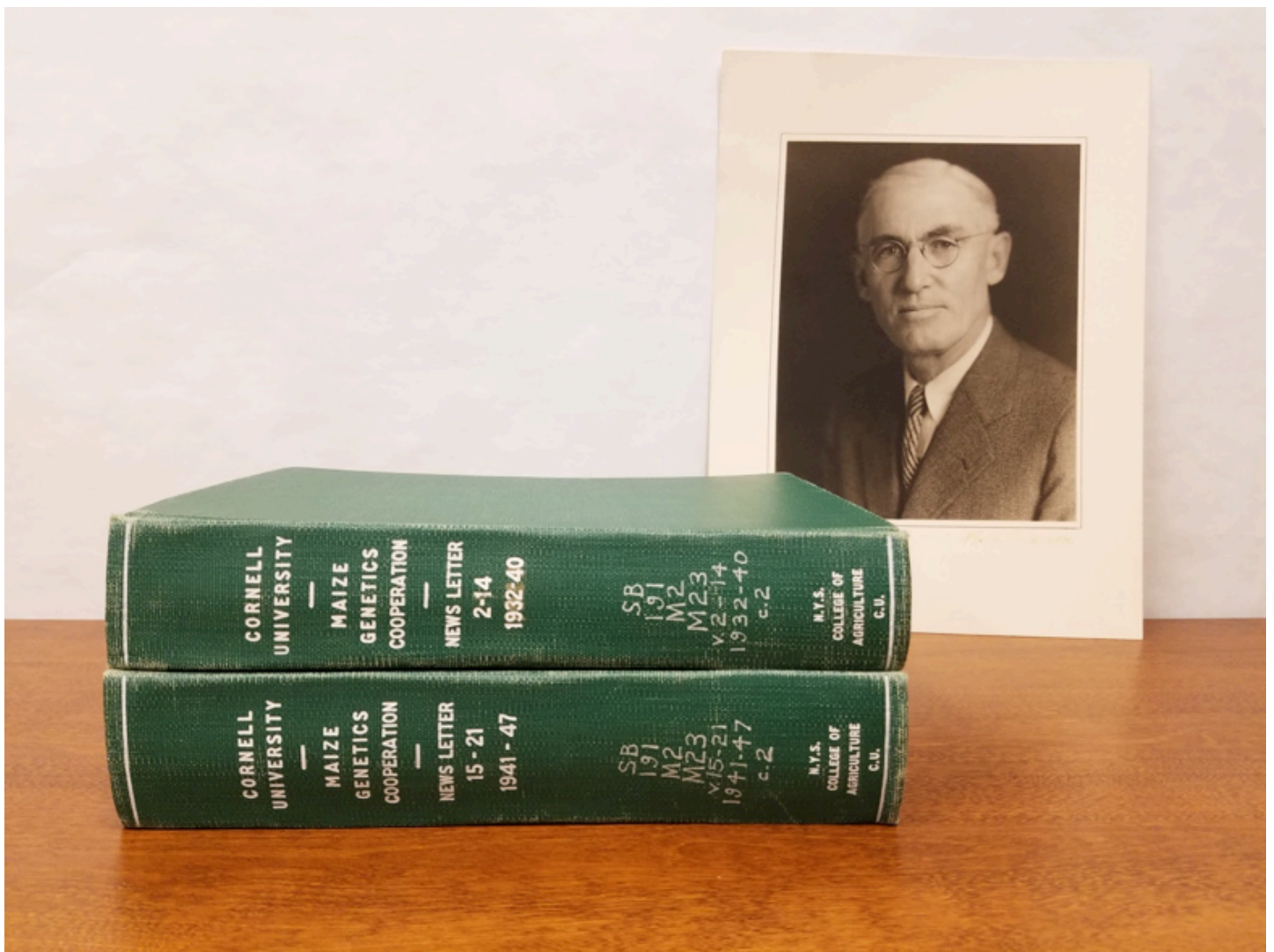
tist at a U.S. institution who has made an extraordinary contribution to agriculture or to the understanding of the biology of a species fundamentally important to agriculture or food production.

Manuscript Reviewer:

Dr. Mark E. Sorrells received his Ph.D. (1977) in Plant Breeding and Plant Genetics from the University of Wisconsin – Madison. After a short post-doc he joined the faculty at Cornell University in the Department of Plant Breeding & Biometry. Since 1991 Dr. Sorrells has been Professor and served as Chair of the Department of Plant Breeding & Genetics at Cornell University (2006-2014). The primary focus of Dr. Sorrells' research program is breeding methodology with application to oat, barley and wheat breeding for the Northeastern region of the United States. He has also been involved in several international projects in Africa, South America, and Europe. During his career Dr. Sorrells has actively developed and evaluated new breeding methods and currently he is integrating genomic selection into his breeding program to reduce pre-harvest sprouting, increase disease resistance and improve yield. Dr. Sorrells has published more than 288 papers in peer-reviewed journals. He has been active in teaching and advising students, serving as major advisor to 45 Ph.D. students, 12 M.S. graduate students and minor advisor to 25 students. He is advisor to Cornell's Synapsis Club, the student-faculty organization founded by H.J. Webber when the Department began in 1907. Sorrells is a Fellow of the Atkinson Center for a Sustainable Future, a Fellow of the Cornell Institute for Food Systems, a Fellow of the Crop Science Society of America, and of the American Association for the Advancement of Science. He is the recipient of the faculty Award for Outstanding Career Accomplishments in Applied Research (2012), College of Agriculture and Life Sciences, Cornell University; the SUNY Chancellor's Award for Excellence in Faculty Service (2015); and of the Outstanding Research Award (2016), of the Crop Science Society of America.



This 1945 Synopsis Club group photo is the last one we have that includes Professor R.A. Emerson (middle row, 3rd from left). Of the seven women in the photo, four on front row [from left, Florence N. Thomas (4), Fung Ting Fung (6), M. Rosalind Morris (7) Leona O. Schnell (8)] received their Ph.D.s with Plant Breeding faculty between 1946 and 1948. (*Reprinted from Murphy & Kass 2011, p. 157; courtesy of Plant Breeding & Genetics and the publisher*)



Maize Genetics Cooperation News Letter volumes 2-14 (1932-1940), and 15-21 (1941-1947), compiled by R.A. Emerson (background), and bound for the former College of Agriculture Library, Cornell University. (Courtesy of Margaret E. Smith, Plant Breeding & Genetics, Cornell University; photo image by Judy Singer)